AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3585, 44 pp., 35 figures, 1 table September 6, 2007

The Chiropteran Premaxilla: A Reanalysis of Morphological Variation and Its Phylogenetic Interpretation

NORBERTO P. GIANNINI[1,2] AND NANCY B. SIMMONS[1]

ABSTRACT

The mammalian premaxilla, which bears the incisor teeth, is composed of a body and two processes (nasal and palatine) that articulate with other rostral bones via four cranial sutures. In bats, the premaxilla is modified in many ways, and this variation has been extensively used in bat systematics. The premaxilla has provided characters to diagnose a number of important taxonomic groupings—most notably, the division of Microchiroptera into the infraorders Yinochiroptera and Yangochiroptera. Recent molecular studies have challenged the monophyly of Microchiroptera, and several families have been transferred to clades other than those in which they were placed traditionally. Because premaxillary characters have figured prominently among those used to establish the traditional classification of bats, we compared the anatomy of the bone across suprageneric bat groups and provide revised descriptions of its variation. On the basis of extensive material examined, we generated 16 new characters, of which at least 12 are partially applicable to all Chiroptera, and several of which are informative within specific bat groups. Three new characters code variation in the basic structure of the chiropteran premaxilla in a new way. As a result, the traditional character defining Yinochiroptera (a "movable premaxilla") was found to lack an anatomical basis; by contrast, Yangochiroptera was still supported. Still, a tree search using just the new premaxillary characters recovered Yinochiroptera as monophyletic. Even with a low character-to-taxon ratio, premaxillary characters recover a number of clades recognized in recent phylogenetic studies of bats. Mapping of characters onto the latest molecular and morphological chiropteran trees required many more extra steps in the former than in the latter. Our interpretation of premaxillary variation in bats suggests two opposing trends in different lineages: one toward weakening and eventual loss of the bone, and the other toward a strengthening

[1] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History (npg: norberto@amnh.org; nbs: simmons@amnh.org).
[2] PIDBA, CONICET, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.

Copyright © American Museum of Natural History 2007 ISSN 0003-0082

via suture fusion. We conclude that, despite some homoplasy, the chiropteran premaxilla is richer in potentially phylogenetically informative characters than previously thought and that it should be explored further in systematic studies of bats at a variety of systematic levels.

INTRODUCTION

The premaxilla is a paired dermal bone located at the apex of the rostrum of the vertebrate skull. It typically bears the anterior teeth, which in mammals are the incisors, and it plays an important functional role in food acquisition and processing. The mammalian premaxilla, or incisive bone (*os incisivum*; fig. 1), is composed of the body (*corpus ossis incisivi*; sometimes called alveolar process), the nasal process (*processus nasalis*), and the palatine process (*processus palatinus*; Evans, 1993). The body of the premaxilla bears the alveoli for the incisors. The nasal process is a roughly vertical, compressed projection from the body that forms the lateral side of the external nasal aperture. The palatal process forms the anteriormost part of the hard palate. Each palatine process typically bears an incisive foramen, which divides the palatine process into a medial flange (running along the midsagittal line) and a lateral flange (running alongside the alveolar line). Most frequently, the caudal edge of each incisive foramen is delimited by the maxilla (fig. 1). The premaxilla participates in four cranial sutures: the interincisive suture (*sutura interincisiva*), nasoincisive suture (*sutura nasoincisiva*), maxilloincisive suture (*sutura maxilloincisiva*), and vomeroincisive suture (*sutura vomeroincisiva*).

This basic plan of the mammalian premaxilla has been significantly modified in many bat lineages, and Chiroptera contains instances of variation not seen in most other mammalian orders. Some aspects of this osteological diversity have been described previously (see Miller, 1907; Andersen, 1912; Wible and Novacek, 1988; Simmons, 1994); and the chiropteran premaxilla has yielded characters of phylogenetic relevance that have been used in bat systematics at a variety of hierarchical levels. Premaxillary morphology has provided synapomorphies for Chiroptera (e.g., Wible and Novacek, 1988; Simmons, 1994) and supported hypotheses of key interfamilial relationships (e.g., Miller, 1907; Koopman, 1985, 1994; Simmons, 1998; Simmons and Geisler, 1998). The division of

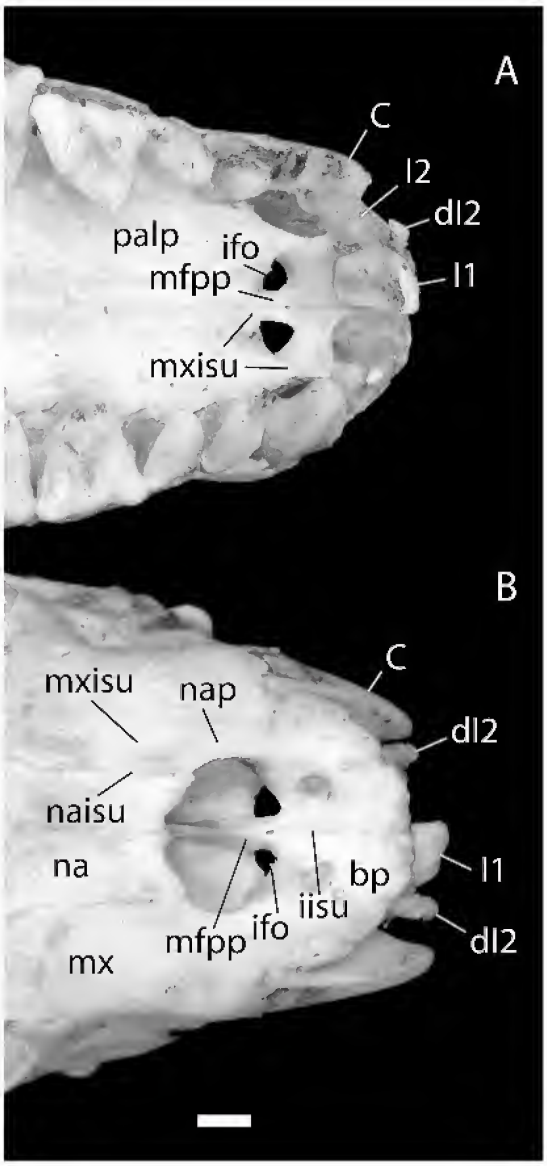


Fig. 1. *Phyllostomus hastatus* AMNH 17032, ventral (**A**) and dorsal (**B**) view of the rostrum showing parts and sutures of the premaxilla. Scale = 1 mm. Abbreviations: **bp** body of premaxilla; **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **dI2** deciduous second incisor; **iisu** interincisive suture; **mfpp** medial flange of palatine process of premaxilla; **mx** maxilla; **mxisu** maxilloincisive suture; **na** nasal; **naisu** nasoincisive suture; **nap** nasal process of the premaxilla; **palp** palatine process of the maxilla.

Microchiroptera into the infraorders Yinochiroptera and Yangochiroptera (Koopman, 1985) was primarily based on differences in premaxillary morphology. According to Koopman (1985, 1994), yinochiropteran bats bear a "movable premaxilla" that is only loosely attached to the maxilla; in contrast, yangochiropteran bats have a premaxillasolidly fused to the maxilla. Premaxillary characters also provide diagnostic characters for many chiropteran families and higher clades, including Craseonycteridae, Megadermatidae, Nycteridae, Rhinolophidae + Hipposideridae, Emballonuridae, Rhinopomatidae, and Noctilionidae (Miller, 1907; Hill, 1963, 1974; Koopman, 1994; Simmons, 1998; Simmons and Conway, 2001). Within families, variation in the premaxilla has proved important in diagnosing genera and species—for instance, in Pteropodidae (e.g., Andersen 1912; Bergmans, 1997), Vespertilionidae (Koopman, 1994), and Molossidae (Koopman, 1994). Giannini and Simmons (2005) used nine premaxillary characters in a combined morphology and DNA phylogenetic analysis of megachiropteran bat relationships.

The aim of this contribution is to study the morphological diversity of the chiropteran premaxilla focusing on the potential phylogenetic utility of observed variation. We show that the variation of premaxillary structures in bats has not been fully documented and that alternative interpretations of structures are necessary. Those interpretations, in turn, affect the ability to diagnose chiropteran clades as currently understood. Our comprehensive descriptions of premaxillary osteology across bat groups facilitates redefinitions of previously described phylogenetic characters as well as accurate definitions of new characters. This analysis has immediate impact on the phylogenetic reconstruction and classification of Chiroptera.

MATERIALS AND METHODS

We studied the osteology of the premaxilla in selected species representing all currently recognized bat families, as well as principal groups within families. We examined articulated premaxillary bones in adult specimens. Depending on the availability of specimens, we complemented our analysis with observations of isolated premaxillae from disarticulated skulls and with images (sequences of slices and three-dimensional renderings) generated from computed tomography (CT)-scanned skulls at the University of Texas High-Resolution X-ray CT Facility in Austin, Texas. (See details of the scanning technique in Rowe et al. [2005] and Macrini et al. [2006].) Low-resolution images of CT-scanned skulls used in this study are available at www.digimorph.org.

Our goal was to describe the structures and relationships determined by the three parts of the premaxilla (body, nasal process, and palatine process) and the four sutures in which the premaxilla participates (incisive, nasoincisive, maxilloincisive, and vomeroincisive sutures), as well as traits that show interspecific variation of importance, such as borders, surfaces, and additional processes of the premaxilla. In adult individuals of many bat species, the premaxilla is fused to neighboring bones (maxilla, nasal, and vomer). Whenever possible, we also examined young and subadult specimens in which the premaxillary sutures were still visible. Anatomical terminology follows Giannini et al. (2006). We examined specimens from the following collections: American Museum of Natural History (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Colección Mamíferos Lillo, Tucumán, Argentina (CML); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Zoology, Baton Rouge (LSU); Royal Ontario Museum, Toronto (ROM); and U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Some specimens are cited in specific context in the family accounts; however, much larger series of specimens were actually examined for the present study.

The observed variation in the form of the premaxilla within Chiroptera far exceeds that known within any other mammalian order and offers great potential for systematic analysis at all taxonomic levels. Toward this end, we define here 16 phylogenetic characters that describe this variation and may be employed in future phylogenetic analyses.

Several premaxillary characters have been used in one form or another in previous phylogenetic analyses; we report prior descriptions and discuss additional observations and modifications, as appropriate. Other characteristics of the upper incisor dentition, such as presence of each tooth, crown structure, and deciduous replacement, are treated elsewhere (Giannini and Simmons, 2007).

Three of the phylogenetic characters proposed here (characters 1–3) describe major alterations in premaxillary form that appear to be informative at higher taxonomic levels. These are each mapped onto the two most complete (in terms of taxonomic and character sampling) existing phylogenies, one based on molecular data (Teeling et al., 2005) and the other based on morphological data (Gunnell and Simmons, 2005). Teeling et al. (2005) used 13.7 kilobase pairs (kbp) from 17 nuclear genes, and Gunnell and Simmons (2005) scored 204 characters from diverse organ systems. Although other molecular and morphological phylogenies are available, they are based on smaller data sets (e.g., Eick et al. [2005] sampled 4 kpb from four nuclear introns and did not include representatives of all bat families) and thus were not employed in the current study. Using the Teeling et al. (2005) and Gunnel and Simmons (2005) phylogenies as frameworks, we compare the homoplasy (extra steps) required by each phylogenetic hypothesis and reconstruct the morphological evolution of the chiropteran premaxilla. In addition, we have included all 16 characters in two phylogenetic analyses. Taxonomic sampling was based on both Teeling et al. (2005) and Gunnell and Simmons (2005); additional taxa were included to represent observed variation in premaxillary characters. Two parsimony analyses were performed, under equal and implied weights, executing in each analysis 200 replications of random addition sequences of taxa, followed by Tree Bisection Reconnection branch swapping. The implied weights analysis (Goloboff, 1993) resolves character conflict in favor of characters with less homoplasy, generally resulting in improved resolution and support (Goloboff et al., in press). The analysis calculates individual character weight by fitting a concave function of homoplasy. Default constant of concavity (k = 3) was used. All analyses were run in the program TNT (Goloboff et al., 2004).

RESULTS

The Premaxilla across Bat Groups

Pteropodidae: In all megachiropterans, the palatine process of the premaxilla is missing altogether (Andersen, 1912). As a result, the incisive foramina coalesce in a single large opening, the incisive fissure (fig. 2; see also Giannini et al., 2006). Interspecific variation in form of the premaxilla is thus limited to the body and nasal process, which are present in all species. Interspecific variation is nevertheless substantial; Giannini and Simmons (2005) identified nine characters of the premaxilla in megabats, which are briefly discussed here.

Several methods have been used to describe the relative width of the nasal process, which is

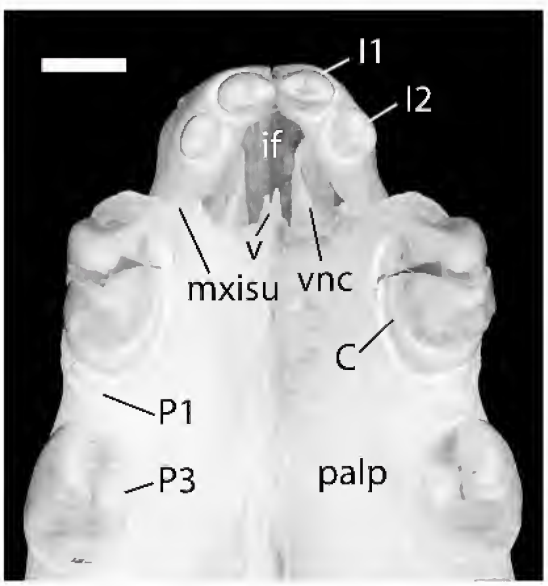
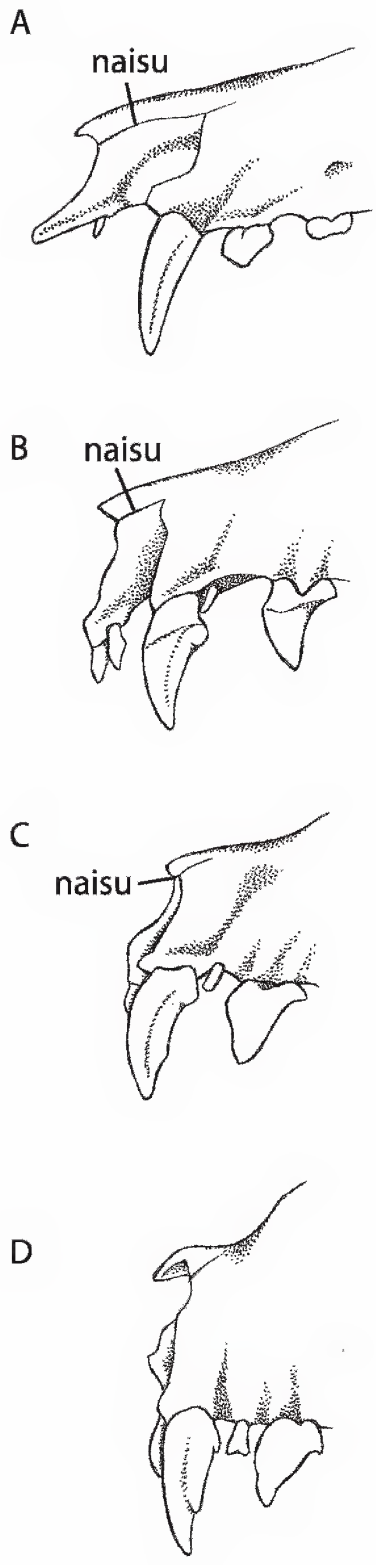


Fig. 2. *Pteropus lylei* CM 87972, ventral view of anterior palate showing incisive fissure. Scale = 2 mm. Abbreviations: **I1** first upper incisor; **I2** second upper incisor; **if** incisive fissure; **C** upper canine; **mxisu** maxilloincisive suture; **P1** first upper premolar; **P3** third upper premolar; **palp** palatine process of maxilla; **v** vomer (incisive incisure); **vnc** ventral nasal concha or maxilloturbinate.



a character long used in megachiropteran systematics (see Andersen, 1912). We find that variation in dorsal width is best reflected in the extent to which the nasal process articulates with the nasal, if it does so at all (Giannini and Simmons, 2005: character 81). The nasoincisive suture is long in *Notopteris* and *Melonycteris* (fig. 3A). Andersen (1912) used this character state in the diagnosis of his Notopterine section, noting that this is the presumed primitive condition in therians. The remainder of megachiropteran genera show three alternative states that reflect degrees of reduction of the nasal process: an intermediate condition in which the nasal process does not distinctly vary in width from its ventral to its dorsal extent and the nasoincisive suture is of intermediate length (e.g., rousettines and pteropodines; fig. 3B); a point contact, in which the premaxilla tapers to a point that just touches the anterior edge of nasals (e.g., in most cynopterines and harpyionycterines, some epomophorines; fig. 3C); and no contact, in which the premaxilla tapers to a point that does not reach the nasal (in nyctimenines; fig. 3D). The caudal edge of the nasal process (the lateral or rostral component of the maxilloincisive suture) may be gently curved, as in most megachiropterans, or it may show a right-angled maxilloincisive suture, as in, for instance, *Pteropus* and *Acerodon* (fig. 4; Giannini and Simmons, 2005: character 82). The anterior edge of the nasal process, or the lateral margin of the external nasal aperture, projects forward in *Nyctimene*, *Paranyctimene*, *Megaerops*, and *Otopteropus*, whereas it does not do so in other genera (Giannini and Simmons, 2005: character 86; see also Mystacinidae, later).

The form of the lateral maxilloincisive suture may change during ontogeny. In

←

Fig. 3. Relative length of the nasoincisive suture in megachiropteran bats (not to scale). The suture is long in *Notopteris* (**A**), of intermediate length in *Pteropus* (**B**), and a point contact in *Cynopterus* (**C**). In *Nyctimene* (**D**), the nasal and premaxilla do not contact each other (interincisive suture absent). Line drawings modified from Andersen (1912). Scale = 5 mm. Abbreviation: **naisu** nasoincisive suture.

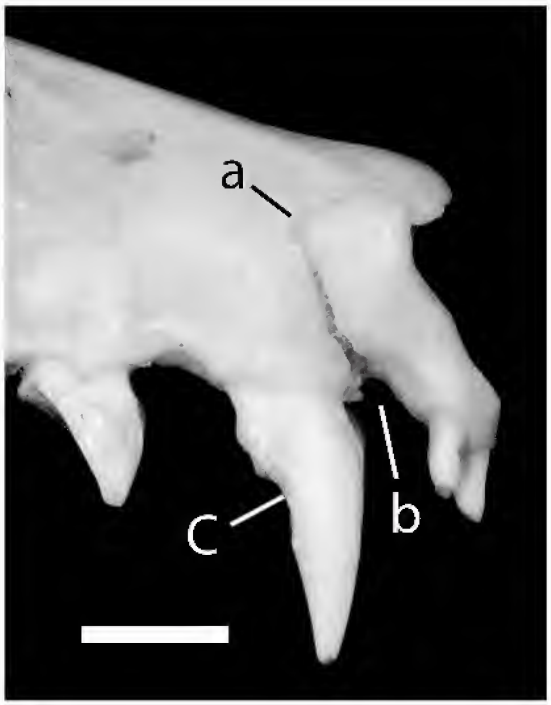


Fig. 4. *Acerodon celebensis* AMNH 153135, lateral view of the anterior rostrum indicating (**a**) angle in the lateral aspect of the maxilloincisive suture and (**b**) notch in the ventrolateral aspect of the same suture. Scale = 1 mm. Abbreviation: **C** upper canine.

juveniles of all megachiropteran species, the nasal process articulates with the maxilla via a foliate suture (sensu Evans, 1993), but this articulation fuses without a trace in some species toward adulthood. Fully adult individuals of *Harpyionycteris*, *Sphaerias*, *Dyacopterus*, *Notopteris*, *Styloctenium*, *Neopteryx*, and *Pteralopex*, as well as old specimens of certain species of *Pteropus*, show premaxillary-maxillary fusion on a regular basis (Giannini and Simmons, 2005: character 84). In one case study (*Pteropus lylei*; Giannini et al., 2006), the maxilloincisive suture is among the last joints to be lost in a lifelong sequence of bone fusion that ends in a skull devoid of distinguishable articulations among elements (other than the obvious exceptions of the cranial synovia, the temporomandibular and atlanto-occipital joints).

The character most commonly cited with respect to the premaxillary body involves the interincisive suture (Andersen, 1912). Based on Andersen (1912), Romagnoli and Springer (2000) used variation in this suture in a phylogenetic context, defining a character with three states: left and right premaxillae not in contact; left and right premaxillae in simple contact anteriorly; left and right premaxillae firmly and solidly ankylosed at early age. Giannini and Simmons (2005: character 78) noted that the variation in the interincisive suture among pteropodids may be better accommodated in four character states: the right and left premaxillary bodies may be widely separated, in this case always accompanied by a medial reduction in the thickness of body (e.g., *Eonycteris major*); the bodies may also be in close contact but not sutured (e.g., *Dobsonia*); or the bodies may be in close contact but sutured (e.g., *Rousettus*); or, finally, the bodies may be fused to each other in fully adult individuals (e.g., *Nyctimene*).

Another character used by Andersen (1912) in his systematic review of megachiropterans is the depth of the body. The body may be thin, barely holding the alveoli of upper incisors, if present (e.g., *Megaloglossus*); intermediate in depth, as in most megabats (e.g., *Rousettus*); or very deep, as in *Nyctimene* and *Megaerops ecaudatus* (Giannini and Simmons, 2005: character 79).

A more controversial character is the so-called proclivity of rostrum—a trait that involves the premaxilla (see previous treatments of this character in Andersen [1912], Springer et al. [1995], and Romagnoli and Springer [2000]). Proclivity of the premaxilla can be defined with respect to the canine root. Two conditions are present in megachiropterans (Giannini and Simmons, 2005: character 80). The anterior edge of the premaxilla may be located at the level of the anterior canine root or surpassing it only slightly—up to the width of an upper incisor (the orthoclivous condition; e.g., *Cynopterus*, fig. 3C), or the anterior edge of the premaxilla may project anteriorly much farther than the width of an upper incisor (the proclivous condition; e.g., *Pteropus*, fig. 3B; *Acerodon*, fig. 4). *Aproteles* lacks upper incisors, but its premaxilla projects only slightly beyond the canine root, which corresponds to the first condition. Under this definition of premaxillary proclivity, *Harpyionycteris* (a

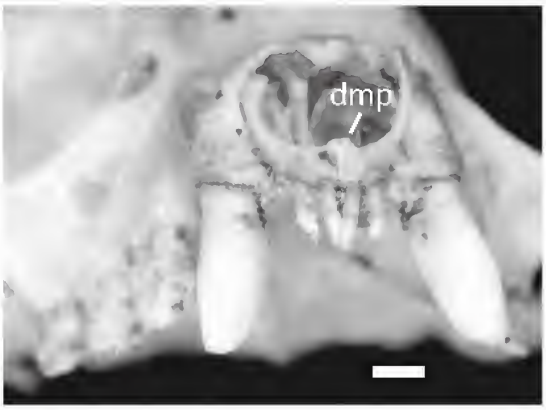


Fig. 5. *Casinycteris argynnis* AMNH 48751, oblique rostrolateral view of the rostrum showing the dorsomedial process of the premaxilla (**dmp**). Scale = 1 mm.

species typically described as having a proclivous rostrum) shows an orthoclivous premaxilla. Only the incisors are proclivous in *Harpyionycteris*, and strongly so, but the premaxilla itself is not with respect to the canines.

The maxilloincisive suture takes two forms in megachiropterans (Giannini and Simmons, 2005: character 85). The most frequent condition is a joint at the level of the canine root, in which an anterior projection of the maxilla reaches the premaxilla bridging the gap between the canine and the second upper incisor (e.g., fig. 3A). An alternative condition is found in *Acerodon* and *Pteropus*, in which a deep gap or vertical notch exists between the alveolar process and the canine root (fig. 4). Finally, the African megachiropterans *Scotonycteris zenkeri* and *Casinycteris argynnis* show a small, upwardly directed process located in the medioventral edge of the external nasal aperture (Giannini and Simmons, 2005: character 83), termed here the "dorsomedial process of the premaxilla". The left and right processes are in contact in the midsagittal line (fig. 5).

EMBALLONURIDAE: In members of this family, the premaxilla lacks a palatine process. As a consequence, an incisive fissure occurs in place of paired incisive foramina. The premaxillary body carries two incisors (in *Emballonura*) or just one (in all other genera); in either case, the small incisors are frequently lost during the life of the individual. Left and

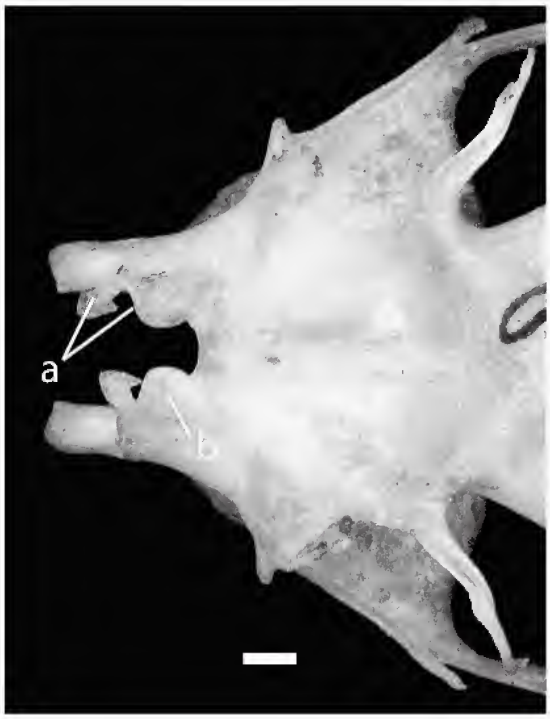


Fig. 6. *Taphozous mauritianus* AMNH 257150, dorsal view of the rostrum showing the twisted medial edge of the premaxilla (**a**) and the proximal pad-like expansion (**b**) typical of the premaxilla of some emballonurids. Scale = 1 mm.

right premaxillary bodies are widely separated, so the interincisive suture is missing. The nasal process is thin and strongly bowed laterally; in rostral view, the external nasal aperture appears rounded. In some genera (e.g., *Peropteryx*, *Saccopteryx*, *Diclidurus*, *Taphozous*), the dorsal end of the nasal process expands into a pad-like flange that projects medially into the external nasal aperture (fig. 6; see later and Dunlop [1998]: character 83 [part]). A less marked dorsal expansion is seen in *Centronycteris*. Finally, the width of the nasal process is uniform throughout its length in *Emballonura*. The premaxilla is loosely attached to the maxilla in emballonurids. The usual foliate structure of the joint (by which the intervening bones interlock) is not present, and the connection of premaxilla and maxilla is via ligaments (a syndesmosis).

Dunlop (1998) used six characters of the premaxilla in her phylogeny of emballonurids;

we discuss them briefly. The overall development of the bone was coded in her character 78, with state 0 indicating a slight reduction of the bone, and state 1, a pronounced reduction "resembling bony splints" (Dunlop, 1998: 79). All emballonurids were scored "1". A problem with this character definition is that the premaxilla is taken as whole, resulting in rather ambiguous character states because components of the premaxilla can be reduced to different degrees. In character 79, Dunlop (1998) coded inclination of the premaxilla against the rostrum in two states—namely, at an angle of 45 degrees (state 0), or "vertical against the anterior rostrum" (state 1; these character states were also used by Lim et al. [2004]: character 27, in a phylogenetic analysis of *Balantiopteryx*). Three genera, *Rhynchonycteris*, *Balantiopteryx*, and *Centronycteris*, were scored "1". However, Dunlop (1998) did not define a horizontal reference (e.g., the rostral axis) to determine the angle, so scoring a new taxon can be problematic. Character 80 reflected the dorsal development of the nasal process—or, more precisely, the absence/presence of a nasoincisive suture. As defined by Dunlop (1998), the premaxillae may contact the nasals (state 0) or they may not (state 1). *Saccolaimos*, some *Taphozous*, and some *Saccopteryx* were scored "0"; in the remainder of emballonurids, the premaxilla does not reach the nasals. In character 81, the lateral edge of the premaxilla, which we interpret as the lateral portion of the maxilloincisive suture, may be curved (state 0) or straight (state 1). Character 82 (also used by Lim et al. [2004]: character 28) coded the shape of the medial edge of the premaxilla, twisted or not. Most emballonurids were scored as having a twisted medial edge of the premaxilla, except *Balantiopteryx*, *Diclidurus ingens*, *Emballonura raffrayana*, *E. monticola*, *E. furax*, *E. beccarii*, and *Mosia*. Finally, Dunlop (1998) coded several conditions of the premaxillary width in her character 83. The premaxilla may widen distally (state 0) or proximally (state 1); it may be of uniform width (state 2); or it may widen both distally and proximally (state 3). Different emballonurids were scored "0" (e.g., some species of *Saccolaimos* and *Emballonura*), or "1" (e.g., species of *Diclidurus*, *Cyttarops*, *Coleura*, *Rhynchonycteris*, *Saccopteryx*, and *Peropteryx*), or "2" (some or all species of *Saccolaimos*, *Mosia*, *Emballonura*, *Balantiopteryx*, and *Cormura*). Again, our decision to treat different parts of the premaxilla separately conflicts with the definition of this character proposed by Dunlop (1998). The distal end of the premaxilla is the body, and the proximal end is the dorsal end of the nasal process; if parts are scored separately, different taxon-character-state associations obtain. For instance, the outgroup *Craseonycteris*, the only terminal scored "3" by Dunlop (1998), shares nothing with emballonurids under her character definition. However, it would share a dorsally widened nasal process with several emballonurids (e.g., *Diclidurus*), as well as a widened body with other emballonurids (e.g., *Emballonura alecto*). Of these states, the dorsal widening (or not) of the nasal process (forming the pad-like flange described earlier) was scored in character 29 of Lim et al. (2004: 228), defined as "premaxilla widens dorsally (state 0) or does not widen dorsally (state 1)". By contrast, width variation of the premaxillary body is complicated by other traits, such as the incisors and the interincisive suture, and is best expressed in terms of variations on those traits (see later).

The premaxilla of one of the best preserved fossils undisputedly assigned to Emballonuridae, the Eocene *Tachypteron franzeni* from Messel, Germany, is well preserved in spite of a largely damaged skull (see Storch et al., 2002: fig 3a). *Tachypteron* resembles modern emballonurids in that "the premaxillae only retain their nasal portion as long thin laminae not fused to the maxillaries nor to each other" (Storch et al., 2002: 192). The premaxilla shows a straight profile without dorsal widening or medial twisting. In general, it is more robust than in extant emballonurids, probably because the two upper incisors are not much reduced.

RHINOPOMATIDAE: As in Emballonuridae, the premaxilla in *Rhinopoma* (e.g., *R. hardwickei* AMNH 219722) lacks a palatine process and has an incisive fissure rather than paired incisive foramina. The premaxillary body is deep and relatively flat; in rostral view, the body and the curved nasal process are lyre-shaped, and the external nasal

Fig. 7. *Rhinopoma hardwickei* AMNH 208125, digital rendering constructed from CT-scan images, rostral view of the rostrum showing the premaxilla and the external nasal aperture. Scale = 1 mm.

Fig. 8. *Craseonycteris thonglogyai* USNM 528306, digital rendering constructed from CT-scan images, dorsal view of the skull, with accompanying line drawing. The fused left and right medial palatine flanges are marked (*). Scale = 1 mm. Abbreviations: **C** upper canine; **c** lower canine; **i1** first lower incisor; **i2** second lower incisor; **I2** second upper incisor.

aperture appears as an inverted teardrop (fig. 7). The body bears a single upper incisor—the second, which marks a subtle jugum (i.e., a relief on the rostral surface of the body caused by the underlying tooth). This incisor inserts obliquely on the side of the body so that the body appears edentulous medially. The left and right bodies barely contact each other at the interincisive suture and remain loosely joined by ligaments. The nasal process is bowed laterally and decreases its width dorsally (fig. 7), tapering to a blunt point that makes contact with the greatly inflated maxillary sinuses but does not reach the nasals.

CRASEONYCTERIDAE: Little can be added to the descriptions of Hill (1974: figs. 3–4) and Hill and Smith (1981: fig. 1). The unique structure of the premaxilla provided characters that justified the segregation of the single species *Craseonycteris thonglongyai* Hill, 1974, in a family of its own. The left and right palatine processes are solidly ankylosed and reduced to a short, tapering spine that reaches less than half the distance from the premaxillary body to the anterior edge of the maxilla, the latter being deeply emarginated (fig. 8). Accordingly, the incisive foramina are partly coalesced, forming an incisive fissure. The left and right bodies of the premaxillae are as deep as the length of the incisors, and the ventral edge of the external nasal aperture is concave. A notch partially separates the left

and right bodies. The left and right nasal processes are slender, expanding dorsally where they fuse to each other to form a rectangular bridge over the external nasal aperture, rostral to the shortened anterior end of the nasals. The rim of the external nasal aperture is thus entirely formed by the premaxillae, which show no trace of a suture at their dorsal point of contact. The premaxilla is loosely attached to the rostrum via ligaments. The shape and attachment of the premaxilla are thought to play a role in supporting the peculiar dermal narial pad distinctive of *Craseonycteris* (Hill, 1974).

MEGADERMATIDAE: This group of five extant species in four genera has often been described as lacking a premaxilla (since at least Miller [1907]). Koopman (1994: 50), when listing the characteristics of the family Megadermatidae, included the "loss of palatal branch of premaxillary and loss or great reduction of its nasal branch". Upper incisors are lacking in megadermatids, an absence correlated with reduction of the premaxilla. Close examination of carefully preserved specimens reveals that *Cardioderma cor* shows a thin splint of bone that corresponds to a nasal process, with a small ventral expansion that represents a greatly reduced but undoubtedly present premaxillary body (fig. 9). The palatine process is entirely lacking in *Cardioderma* (fig. 9). Our examination of the other four species of megadermatids failed to detect any trace of ossified premaxillary elements. We could not attribute this to poor specimen conservation in all cases, as many of the specimens available to us were very well prepared. Accordingly, we conclude that premaxillary elements are entirely absent in *Lavia*, *Macroderma*, and *Megaderma*. CT-scanned images of *Lavia frons* AMNH 49384 further confirm this observation.

HIPPOSIDERIDAE: Members of this family (see also Rhinolophidae, later) lack the nasal process of the premaxilla and have the body and palatine processes widely separated from the maxilla laterally, so the narrow premaxilla attaches to the maxilla only via a restricted caudal joint (fig. 10). The body forms a shallow bar that supports the small incisors and is continued caudally in the well-developed palatine process that consists only of its medial flange. The left and right palatine processes are in close medial contact along their length.

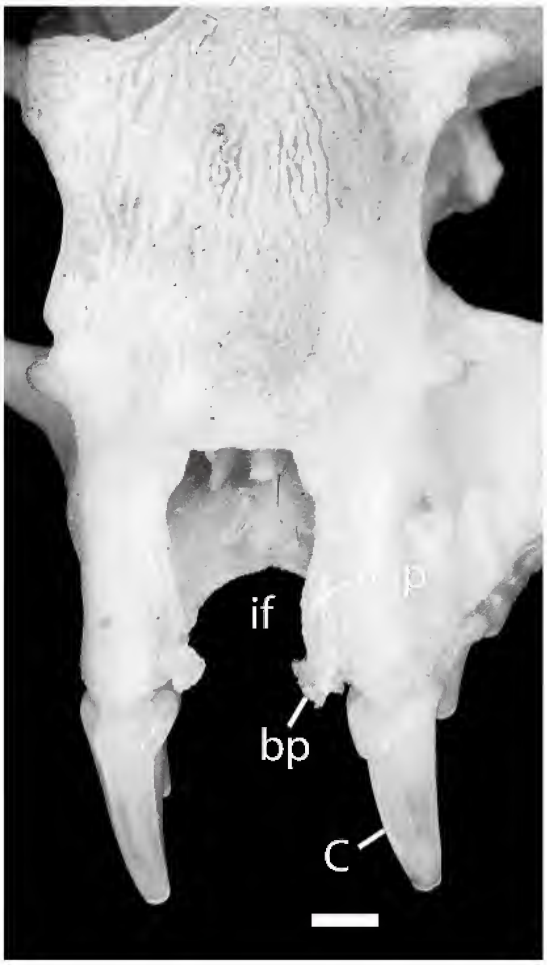


Fig. 9. *Cardioderma cor* AMNH 184336, oblique view of the rostrum showing reduced premaxilla. Scale = 1 mm. Abbreviations: **bp** body of premaxilla; **C** upper canine; **if** incisive fissure; **nap** nasal process of the premaxilla.

The incisive foramina are of particular interest. A common mammalian condition, present in many bats (but see Noctilionidae), is that the incisive foramen (or fissure) is limited rostrally, medially, and laterally by the premaxilla and caudally by the maxilla (fig. 1). In some species of *Hipposideros* (e.g., *H. gigas*), the incisive foramina are completely embedded in the substance of the palatine process, which surrounds the foramina posteriorly as well as anteriorly, medially, and laterally (Hand and

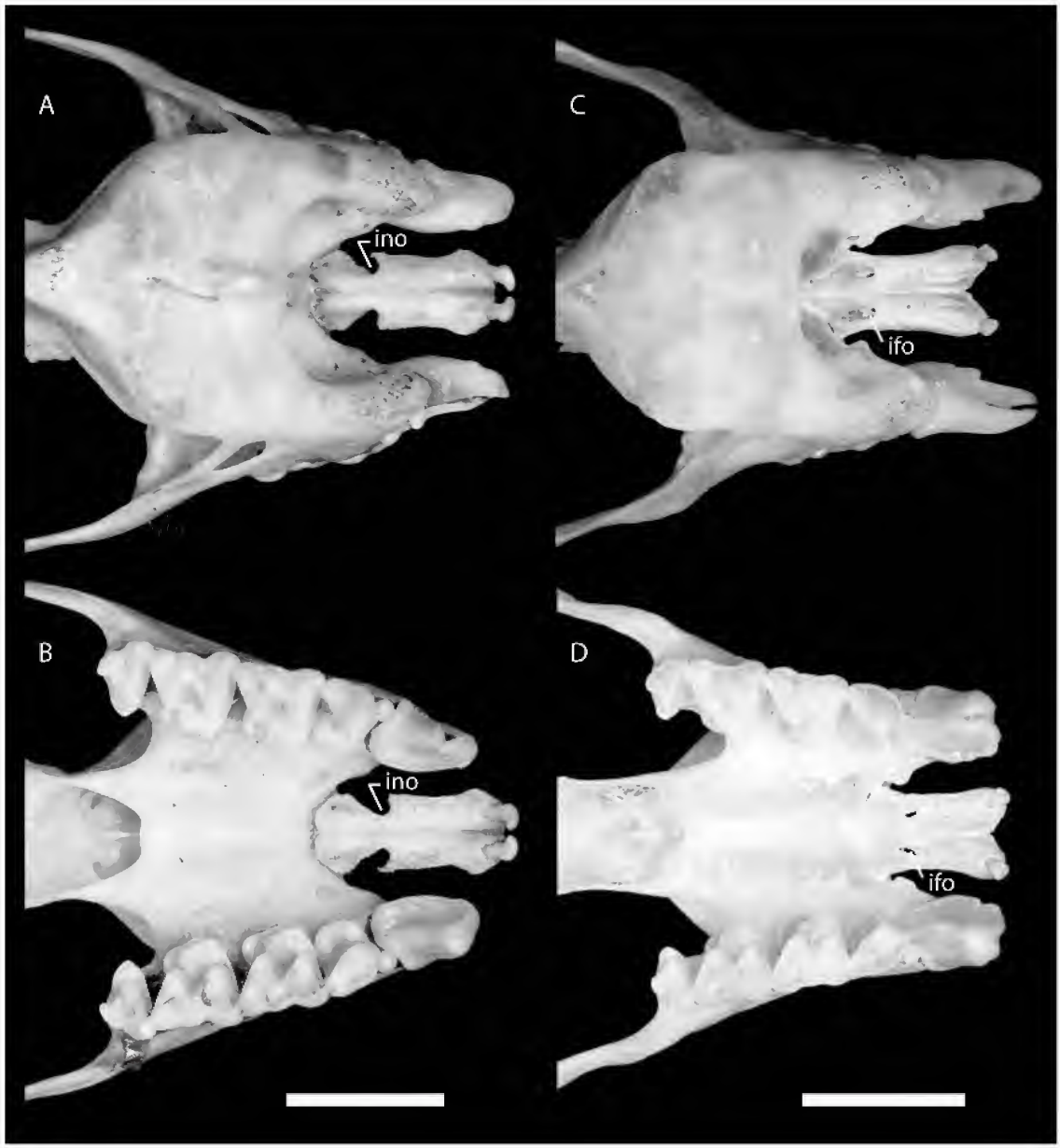


Fig. 10. *Hipposideros armiger* AMNH 216949 (**A**, **B**) and *Hipposideros gigas* AMNH 241044 (**C**, **D**.). Dorsal (**A**, **C**) and ventral (**B**, **D**) views of the rostrum showing the premaxilla and its wide medial attachment to the hard palate (cf. *Triaenops* in Fig. 11). Scale = 5 mm. Abbreviations: **ifo** incisive foramen; **ino** incisive notch.

Kirsch, 1998: character 9). In the alternate condition, present in many *Hipposideros* (e.g., *H. armiger*) and in all species of the other hipposiderid genera, an incisive notch is present—i.e., the incisive foramen is not completely enclosed in the palatine process. A comparison of the two conditions is provided in figure 10. Hand and Kirsch (1998) found this notched condition in seven species of *Hipposideros* (out of 23 scored) from five different species groups (i.e., *cyclops*, *diadema*, *larvatus*, *speori*, and *pratti* species groups as recognized by Simmons, 2005). As a consequence of its rather scattershot distribution, this

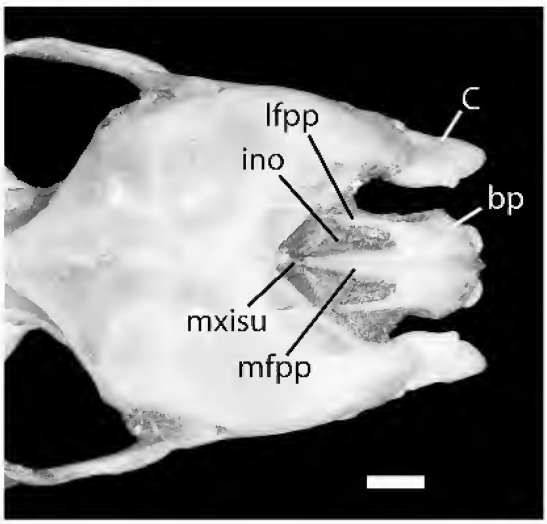


Fig. 11. *Triaenops persicus* AMNH 216287, dorsal view of the rostrum showing the premaxilla and its medial point contact with the maxilla (cf. *Hipposideros* in fig. 9). Note preserved soft tissue flooring the nasal cavity between the premaxilla and maxilla. Scale = 1 mm. Abbreviations: **bp** body of premaxilla; **C** upper canine; **ino** incisive notch; **lfpp** lateral flange of palatine process of premaxilla; **mfpp** medial flange of palatine process of premaxilla; **mxisu** maxilloincisive suture (point contact).

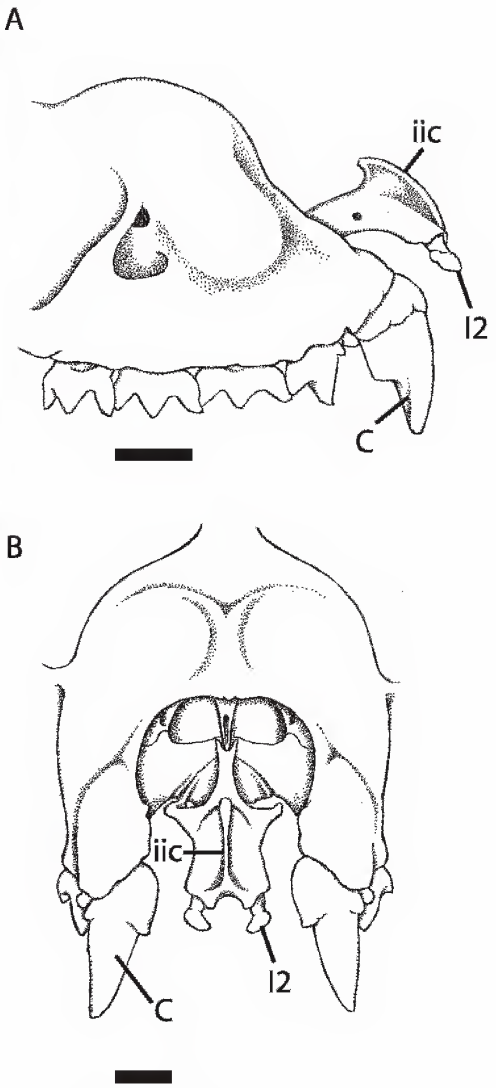


Fig. 12. *Rhinonicteris aurantius* AMNH 197216, lateral (**A**) and oblique rostrodorsal (**B**) view of the rostrum showing the interincisive crest of the premaxilla. Scale = 1 mm. Abbreviations: **C** upper canine; **I2** second upper incisor; **iic** interincisive crest.

character did not contribute a single synapomorphy in Hand and Kirsch's (1998) study.

The incisive foramen or notch in hipposiderids is accompanied by a sulcus that runs along the ventral side of the palatine process. In species with embedded foramina, the sulcus is part of a canal whose caudal end opens on the dorsal side of the hard palate, whereas its rostral end opens on the ventral side of the hard palate. The contents of that canal are unknown; we speculate that such contents may be the same as those found in another bat, *Pteropus* (Giannini et al., 2006)—i.e., the nasopalatine duct, the septal branches of the caudal nasal nerve of V2, and no major vessel.

The articulation of the medial palatine process with the maxilla consists of a point contact in some hipposiderid genera (e.g., *Aselliscus*, *Triaenops*; fig. 11). In other genera, including *Hipposideros* (fig. 10), the process contacts caudally with the entire front of the rostral edge of the palatine process of the maxilla. In *Rhinonicteris*, a suture is evident between the medial and lateral flanges of the palatine process (the latter reduced to splints of bone), suggesting a secondary caudal closing of the incisive foramina by premaxillary tissue.

Some hipposiderids show a distinct keel, which we term the "interincisive crest", that is formed by the medial union of laminar expansions from the left and right palatine process dorsal to the interincisive suture (fig. 12).

Bogdanowicz and Owen (1998) used this trait as a binary character in a phylogenetic analysis of the family, scoring *Rhinonicteris aurantius*, *Triaenops furculus*, *T. persicus*, and *Cloeotis percivale* as having a "hornlike crest in middle of dorsal part of premaxillae" (Bogdanowicz and Owen, 1998: 38, character 1). Similarly, Hand and Kirsch (1998) used an equivalent character defined as "Premaxillae: (0) not especially thickened; (1) very thick with distinct crest on dorsal surface at line of contact" (Hand and Kirsch, 1998: 85, character 10). Hand and Kirsch (1998) identified *Triaenops persicus*, *Rhinonicteris aurantius*, and the Australian early Miocene *R. tedforti* and *Brachipposideros nooraleebus* as having state 1, but *Cloeotis percivale* was scored "0". In his revision of the group, Hill (1982: 168) noted a "distinct ridge on the upper face" of the premaxillae as occurring in *Rhinonicteris* and *Triaenops* but not in *Cloeotis*. In our sample, we observed that in *Cloeotis percivale* (e.g., AMNH 168161), an interincisive crest is present. As in *Triaenops* (e.g., *T. persicus* AMNH 216237), the crest in *Cloeotis* is much shorter than the crest of *Rhinonicteris* (e.g., *R. aurantius* AMNH 1972113, 197216, fig. 12) but is nonetheless present.

The presence of the interincisive crest supported a clade formed by *Brachipposideros* and *Rhinonicteris* when characters were unordered in the morphological analysis of Hand and Kirsch (1998). *Triaenops* and two fossil genera (the Australian early Miocene *Riversleigha* and *Xenorhinos*) joined that clade if characters were ordered (Hand and Kirsch, 1998). Interestingly, the premaxilla is unknown in *Riversleigha* and *Xenorhinos* (scored "?" in Hand and Kirsch, 1998: characters 9–10). Therefore, the recovery of these fossils nested within this clade predicts the presence of an interincisive crest in these forms. Note that if *Cloeotis* is scored "1" for this character, the presence of the interincisive crest diagnoses a larger clade inclusive of this form plus *Coelops* (represented by *C. frithi*), in which the absence of interincisive crest would represent a reversal (see Hand and Kirsch, 1998: fig. 5.1b).

Within *Hipposideros*, Hill (1963: 9) described the variation in premaxillary characters as follows (our synonymy in square brackets):

Considerable variation is displayed in the form of the premaxillae, which basically form a projecting structure with a V-shaped or U-shaped junction with the maxillae [= maxilloincisive joint, palatine part]. Considered together, they vary from a narrow oblong structure not greatly expanded posteriorly at its junction with the maxillae to a wide structure almost filling the anterior palatal emargination with a wide, sometimes fan-shaped union with the maxillae. Their lateral edges may be deeply notched so that with the maxillae they form the walls of the anterior palatal foramina [= incisive foramina]. In some species, delicate anterior enclosing processes [= lateral flange of the palatine process] are developed to form the anterior walls of these foramina: these processes in other species completely enclose the foramina which are thus contained within the premaxillae. The anterior palatal foramina in some species are small and rounded and in others are large and oval, elongate or slit-like.

Finally, two conditions of the premaxillary body are found in *Hipposideros*. The diastema between the single left and right incisor may be straight and flat, as in *H. armiger* (e.g., AMNH 216949), or a small recess may be present in the body between the incisors, as, for instance, in *H. gigas* (e.g., AMNH 241044; see fig. 10).

Rhinolophidae: The premaxilla in *Rhinolophus* is very similar to that of *Hipposideros* (cf. figs. 10, 13, 14). The incisive foramina (notches) are variably included in the substance of the palatine process and may open to the caudolateral side of the palatine process, as in *Rhinolophus ferrumequinum nippon* AMNH 245591 (fig. 13), or the incisive notches may be closed caudally by the medial convergence of lateral flanges (e.g., *Rhinolophus alcyone* AMNH 236298; fig. 14). The ventral sulcus seen in hipposiderids is also present in *Rhinolophus* (e.g., *R. alcyone* AMNH 269922; *R. ferrumequinum* AMNH 160473; *R. hildebrandti* AMNH 161917).

Nycteridae: As in hipposiderids and rhinolophids, in this family the nasal process of the premaxilla is entirely lacking. The nycterid premaxilla can be described as a sloping body that is continued caudally, forming a wide obtuse angle, by the roughly horizontal,

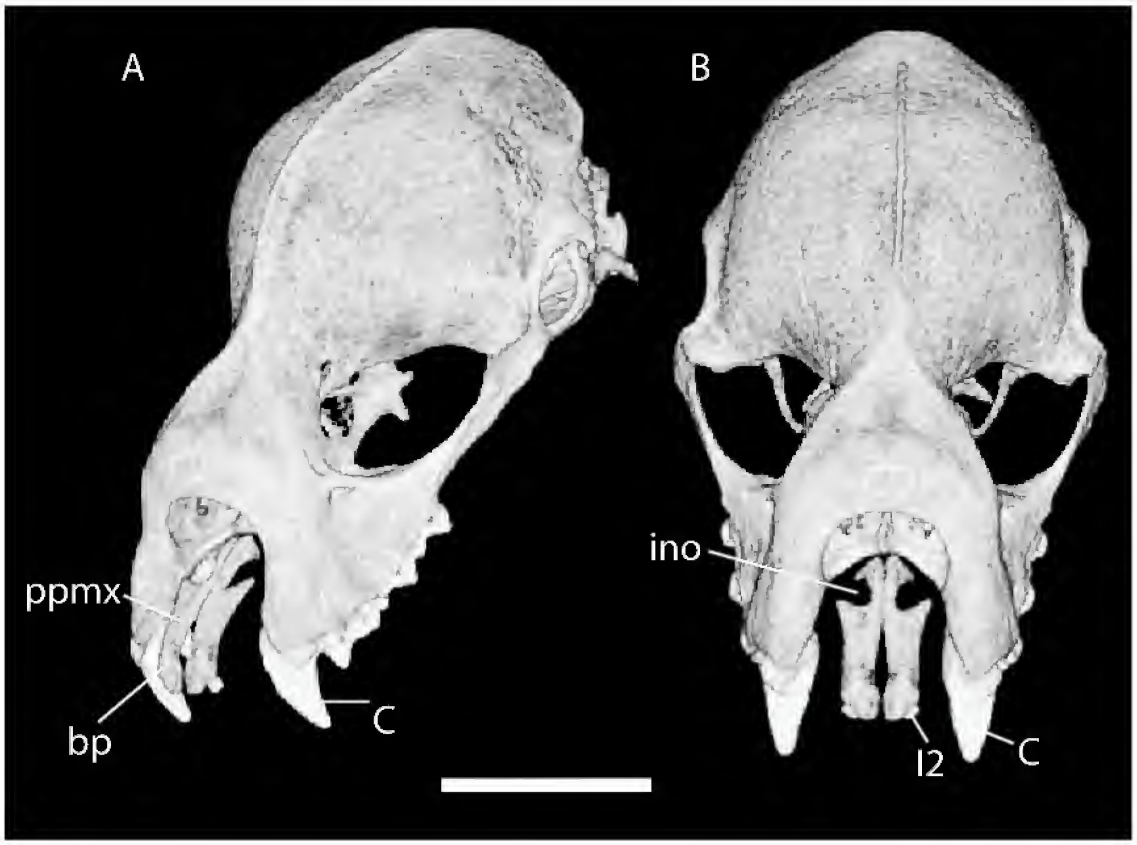


Fig. 13. *Rhinolophus ferrumequinum nippon* AMNH 245591, digital rendering constructed from CT-scan images, rostrodorsolateral (**A**) and rostrodorsal (**B**) views of the skull. Scale = 5 mm. Abbreviations: **bp** body of premaxilla; **C** upper canine; **I2** second upper incisor; **ino** incisive notch; **ppmx** palatine process of premaxilla.

laterally diverging palatine process (fig. 15). The left and right bodies are separated from the maxillae by a lateral gap, and articulate with each other via ligaments. Each body bears the alveoli for two small incisors. The body is barely deeper than the incisor roots, which are recurved dorsocaudally to accommodate their lengths in the short body. Apparently, the palatine portion of the premaxilla corresponds to the lateral palatine flange seen in other bats. This conclusion is based on the fact that the palatine laminae diverge caudolaterally from the sagittal plane, encompassing a single large incisive fissure (contra Miller, 1907). In this interpretation, *Nycteris* lacks the medial flange of palatine process, differing in this way from the superficially similar premaxilla of hipposiderids and rhinolophids, in which the medial flange is well developed. The premaxilla abuts the maxilla caudolaterally, forming an overlying edge to which ligaments are attached (fig. 15).

Within nycterids, variation exists in the interincisive suture. The left and right premaxillary bodies may be in contact, as in *N. grandis* (e.g., FMNH 151186; fig. 15), or the bodies may be partially separated, as in *N. thebaica* (e.g., AMNH 213046). It is interesting to note that in the latter, the first upper incisors converge medially, even though the left and right bodies are separated, thus forming a continuous incisor row despite the separation in the supporting bones.

MYSTACINIDAE: The premaxilla in *Mystacina* is complete in that it possesses a body and the palatine and nasal processes are both well

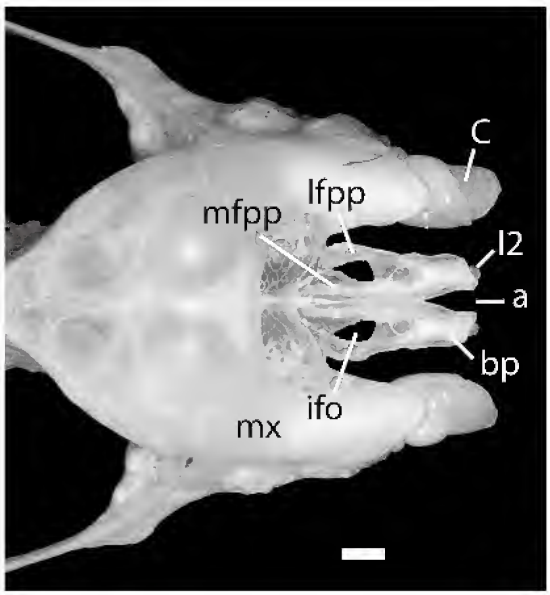


Fig. 14. *Rhinolophus alcyone* AMNH 236298, dorsal view of the rostrum. Scale = 1 mm. Abbreviations: **a** wedge-shaped gap between left and right premaxillary bodies; **bp** body of the premaxilla; **C** upper canine; **I2** second upper incisor; **ifo** incisive foramen; **lfpp** lateral flange of the palatine process of the premaxilla; **mfpp** medial flange of the palatine process of the premaxilla; **mx** maxilla.

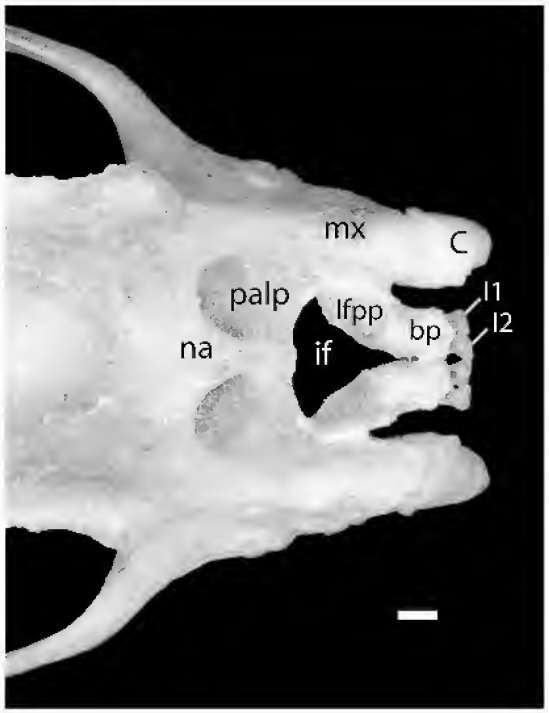


Fig. 15. *Nycteris grandis* FMNH 151186, dorsal view of the rostrum. Scale = 1 mm. Abbreviations: **bp** body of premaxilla; **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **if** incisive fissure; **lfpp** lateral flange of palatine process of premaxilla; **mx** maxilla; **na** nasal; **palp** palatine process of the maxilla.

developed (e.g., *Mystacina robusta* AMNH 160269, 214243; *M. tuberculata* 173919, 174825). The left and right premaxillae are fused to each other and to the maxilla. The nasal process is wide and reaches the nasals, but the nasoincisive suture is short (fused in adults). The nasal process exhibits an expansion of its rostral edge, so the processes are projected forward (fig. 16A; see also Pteropodidae). Thus, in lateral view, the external nasal aperture has the appearance of a short tube. The depth of the body varies: at the interincisive suture, the left and right bodies are relatively narrow. In spite of this, the root of the large I1 is very long and takes a divergent dorsal course, running parallel to the lateral edge of the external nasal aperture up to one half the height of the aperture (fig. 16A).

The medial flange of the palatine process is present and separates two very small incisive foramina. An unpaired, medial accessory palatine foramen of similar size but unknown content is present rostral to the paired incisive foramina.

NOCTILIONIDAE: In *Noctilio*, the nasal processes of the premaxilla are wide and are fused with the nasal bones dorsally and with the rostral processes of the maxilla posterolaterally. The nasal processes are projected rostrally, as described for *Mystacina*, but this condition is especially well marked in *Noctilio albiventris* (fig. 16B). Also as in *Mystacina*, the root of the large I1 is divergently directed dorsally in both species of *Noctilio*, running parallel to the lateral edge of the external nasal aperture. Both *Noctilio albiventris* and *N. leporinus* show a notch in the premaxilla where the lower canine fits, but this notch is markedly larger in the latter (e.g., *N. leporinus* FMNH 58122); in addition, the small size and crowded position of I2

contributes to the large, arched diastema between I2 and C. A low ridge is present just above the diastema and I2. *Noctilio albiventris* lacks the ridge, and the diastema is proportionally smaller.

Adult specimens of both *Noctilio* species lack incisive foramina. Simmons and Conway (2001) used this trait as a phylogenetic character and cited it as a synapomorphy diagnosing Noctilionidae. The absence of patent incisive foramina of any kind makes it difficult to establish the homology of the continuous bony lamina that covers the anterior palate in *Noctilio*. However, an examination of juveniles (*Noctilio albiventris* AMNH 79651, 79673) indicates that the incisive foramina are present at early age and are separated by a thin and short medial flange of the palatine processes (fig. 17). At the stage of AMNH 79673, the maxilla already bears a crescent-shaped, rostrally oriented process that underlies the incisive foramen, termed here the "incisive process of the maxilla". Eventually, this process closes the incisive foramen (e.g., in AMNH 79651), later fusing with the premaxilla and sealing the anterior palate. As a consequence, *Noctilio* possesses lateral and medial flanges of the palatine processes and lacks incisive foramen or fissure due to the growth of an anteriorly directed incisive process of the maxilla. Premaxilla and maxilla are seamlessly fused in adult specimens of *Noctilio*.

MORMOOPIDAE: In most species of *Pteronotus*, including the Cuban fossil *P. pristinus* (e.g., ROM 59132; see Simmons and Conway, 2001), the premaxilla is remarkably similar to that of *Mystacina* in all respects (fig. 16C). *Pteronotus personatus* and the two species of *Mormoops* differ in that the rostral edges of the nasal processes are not distinctly projecting. *Mormoops* further differs in that the medial accessory palatine foramen is lacking (see Simmons and Conway, 2001).

←

Fig. 16. *Mystacina tuberculata* AMNH 173919 (**A**), *Noctilio albiventris* AMNH 243904 (**B**), and *Pteronotus parnelli* AMNH 269063 (**C**), digital rendering constructed from CT images, rostrolateral view of the rostrum showing the premaxilla produced as a short tube. Scale = 1 mm.

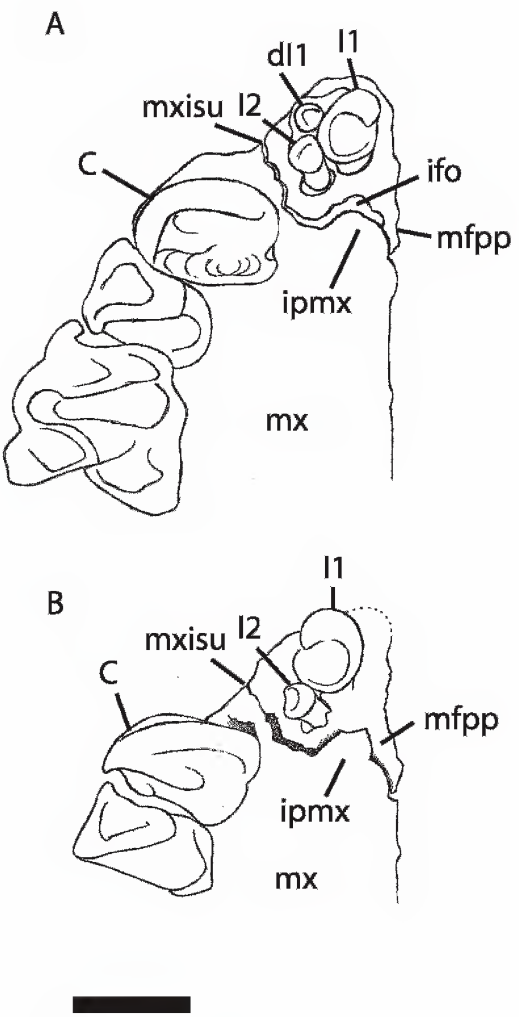


Fig. 17. *Noctilio albiventris* AMNH 79673 (**A**) and AMNH 79651 (**B**), ventral view of the right hard palate showing the inferred process of closing the incisive foramen by the incisive process of the maxilla. Scale = 0.5 mm. Abbreviations: **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **ipmx** incisive process of the maxilla; **mfpp** medial flange of the palatine process of the premaxilla; **mx** maxilla; **mxisu** maxilloinsive suture.

Simmons and Conway (2001) used three premaxillary characters from Simmons and Geisler (1998) in their phylogenetic analysis of Mormoopidae. These characters were not informative within Mormoopidae but were used for outgroup comparisons. These characters reflected the fusion of the premaxilla to the maxilla (their character 1, state 0), the presence of the palatine process (character 2, state 0), and the presence of incisive foramina (character 3, state 0).

PHYLLOSTOMIDAE: Members of this family generally have the nasal process of the premaxilla fused to the maxilla and nasal and the left and right bodies fused to each other. The medial flange of the palatine process is present, so the incisive foramina are well delimited. Three aspects of the phyllostomid premaxilla are remarkable. First, the medial flange of the palatine processes may contact the maxilla in the usual way (i.e., articulating with the maxilla at the level of the palatal shelf), or the medial palatal process may instead articulate above the level of the palatine shelf, bypassing the rostral edge of the palatine process of the maxilla (fig. 18). The latter condition is found in several genera (e.g., *Vampyrodes*, *Carollia*), and in some of these (e.g., *Platyrrhinus*) there is a prominence of the maxilla (with a corresponding vault in the palate) that acts as a platform supporting both the vomer and the caudal edge of the medial flange of the palatine process (fig. 18).

Carstens et al. (2002) scored the presence of an unnamed "third" foramen in the premaxilla of some glossophagines (their character 4, state 1), an alternative condition to the presence of just two foramina (i.e., the paired incisive foramina; their character 4, state 0). This unpaired opening (fig. 19A) corresponds to our accessory incisive foramen (see *Mystacina*), which is anteromedial to the paired incisive foramina. The accessory incisive foramen occurs in several phyllostomid genera, sometimes accompanied by nutrient foramina located anterior or posterior, dorsal or ventral to it—a trait that exhibits high intraspecific variation. The medial accessory foramen, present also in some other yangochiropterans (e.g., *Mystacina*, *Pteronotus*), may be the remainder of the secondary closing of a rostral wedge-shaped gap between left and right bodies (see *Myzopoda*). This conclusion is based on observations of some phyllostomids with weakened premaxillary bodies due to reduced dentition (e.g., *Anoura caudifer* CML 5493, *Anoura geoffroyi* AMNH 263192 [fig. 19A], *Choeroniscus minor* AMNH 267948 [fig. 19B]).

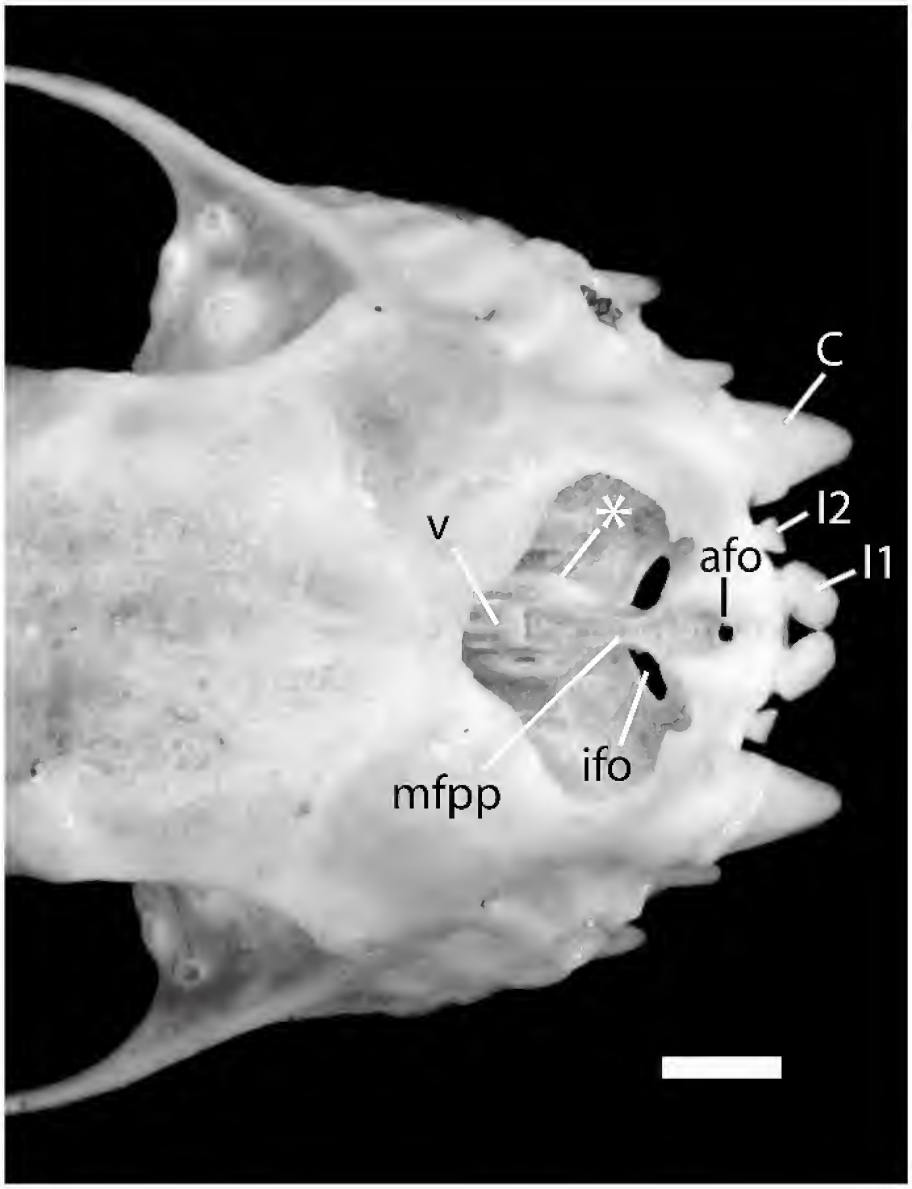


Fig. 18. *Platyrrhinus helleri* AMNH 267182, dorsal view of the rostrum. Indicated with (*) is the maxillary platform that receives both the vomer caudally and medial flange of the palatine process of the premaxilla rostrally. The presence of an accessory medial foramen is also notable. Scale = 1 mm. Abbreviations: **afo** accessory medial foramen; **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **mfpp** medial flange of the palatine process of the premaxilla; **v** vomer (incisive incisure).

Many phyllostomids (e.g., *Carollia perspicillata* AMNH 266126; see fig. 20) show the same pattern of long I1 roots penetrating high up in the lateral edge of the external nasal aperture that was noted previously in Mystacinidae and Noctilionidae. However, the reverse pattern is seen in other phyllostomids in which I2 is greater than I1 so that the I2 root is the one that penetrates vertically into the substance of the premaxilla (e.g., *Anoura geoffroyi* AMNH 263193).

Examination of available juvenile specimens from species representing three different subfamilies (*Phyllostomus hastatus* AMNH 17034

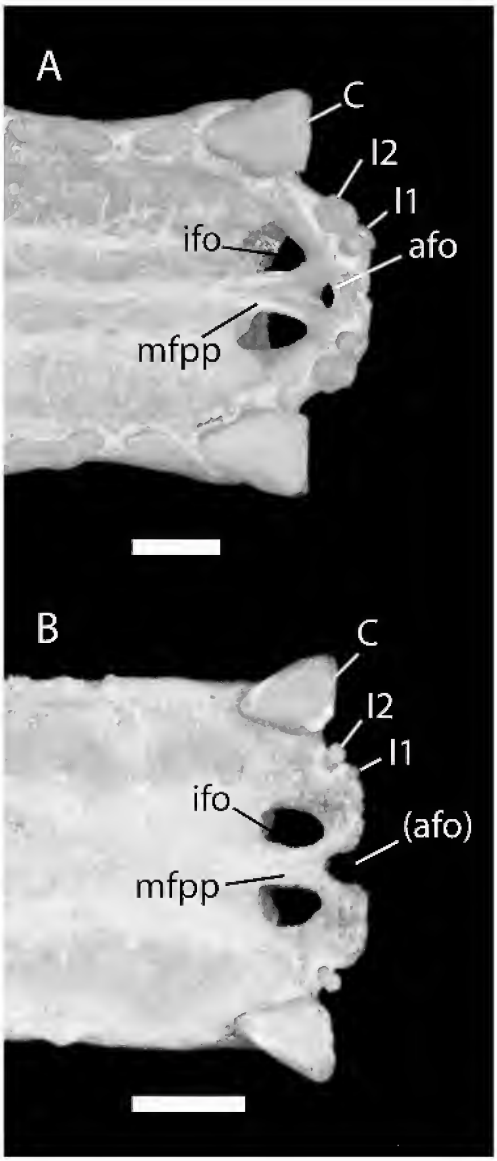
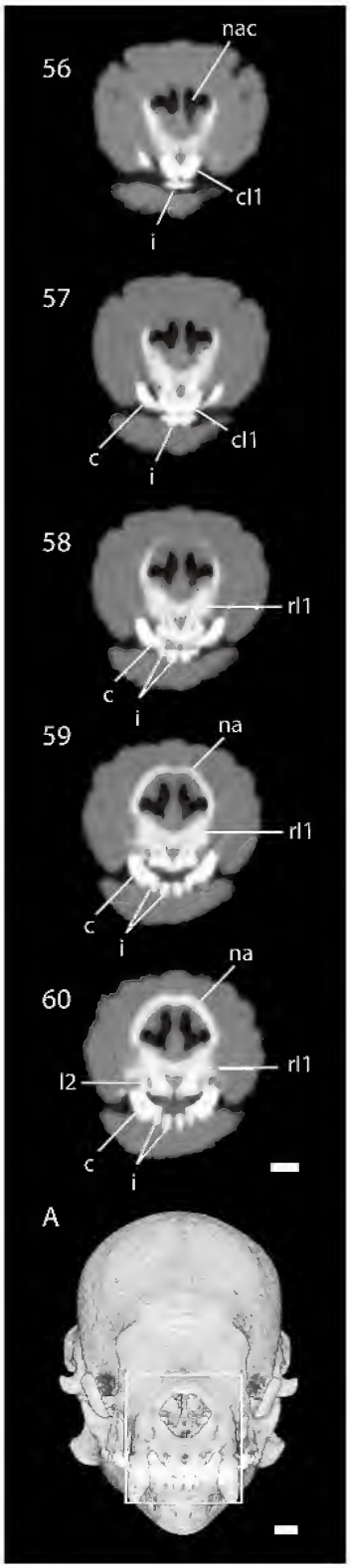


Fig. 19. *Anoura geoffroyi* AMNH 263192 (**A**) and *Choeroniscus minor* AMNH 267948 (**B**), ventral view of the anterior palate showing the possible homology of the accessory medial foramen and the wedge-shaped gap caused by reduction of insicsors and the concomitant weakening of the premaxillary body. Scale = 1 mm. Abbreviations: **afo** accessory medial foramen (parentheses indicates presumed homology); **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **mfpp** medial flange of the palatine process of the premaxilla.

[Phyllostominae], *Anoura caudifer* CML 3146 [Glossophaginae], and *Artibeus lituratus* AMNH 76677 [Stenodermatinae]) suggests that the nasal processes are long in phyllostomids, abutting the nasals laterally and tapering to a point at the anterior third of the nasal length. Thus, the lateral side of the external nasal aperture is completely delimited by the nasal process, and the nasoincisive suture is very long, reaching well caudad to the level of the upper canine. The maxilloincisive suture may remain visible in adult specimens of some nectar-feeding bats (e.g., *Scleronycteris*). Other variations observed in long-nosed nectar-feeding bats (e.g., *Anoura caudifer*) include the presence of a depression between the upper canine jugum and the nasal process of the premaxilla and a wide I1-I1 diastema derived from reduction of the bulk of incisors.

Important shape variation occurs in relation with rostral length and shape in phyllostomids. Premaxillary proclivity is marked in some nectar-feeding taxa (e.g., Lonchophyllini), with the premaxilla accompanying the general elongation of the rostrum seen in those bats. Gregorin and Ditchfield (2005) showed an interesting increase in proclivity within Lonchophyllini, from a moderate condition in *Lionycteris* to an extreme case in *Xeronycteris*, in which proclivity is so marked that the orientation of I1 is almost horizontal with respect to the alveolar line. At the other end of the spectrum are fruit specialists in the Stenodermini, which show extreme shortening of the rostrum and caudal displacement of the external nasal aperture. For instance, *Centurio* exhibits a premaxilla that is orthoclivous with respect to the level of the upper canine. In *Ametrida* and *Sphaeronycteris*, the premaxilla is affected by the extreme retraction of the external nasal aperture and the upturning of the rostrum; as a consequence, the body of the premaxilla is strongly slanted dorsocaudally. Wetterer et al. (2000) contrasted this condition (their character 47, state 1) with the gently sloping rostrum of most phyllostomids (state 0), in which the nasal process of the premaxilla is not significantly inclined and lies roughly perpendicular to the palatine process. Surprisingly, seemingly opposite morphogenetic processes (extreme elongation versus re-



traction of the rostrum) produce a similar effect in the orientation of the premaxilla.

In another group of dietary specialists, the blood-feeding Desmodontinae (vampire bats), the premaxilla has a triangular shape in ventral view as it bears large, blade-shaped incisors that converge rostrally and are used to cut the skin of birds and mammals to obtain blood. The medial flanges of the palatine processes are very thin, and the incisive foramina are large. Also, the premaxilla is elevated with respect to the maxillary alveolar line, which effectively separates the large incisor blades from the upper canines (fig. 21).

MYZOPODIDAE: All of the premaxillary components are present in *Myzopoda aurita*. In adult individuals (e.g., USNM 449282), the left and right bodies decrease in height medially and are well separated by a wedge-shaped gap—a moderate "anterior palatal emargination" sensu Simmons and Geisler (1998; their character 13, state 1, and character 14, state 0; see fig. 22). The body of the premaxilla bears two incisors, with I1 being significantly smaller than I2. The alveolus of I1 is short and obliquely displaced dorsolaterally. The nasal process of the premaxilla is fused to the maxilla laterally; the relationship of this process with the nasal is not clear due to early bone fusion. The palatine process of the premaxilla is fused to the maxilla and vomer medially and is rostrally connected to the body via a thin bar of bone (fig. 22). This obliquely oriented bar closes the incisive foramen anteriorly. A relatively small, kidney-shaped incisive foramen divides the palatal process into a thick medial flange and

←

Fig. 20. *Carollia perspillata* AMNH 266126, sequence from 56 to 60 coronal CT images through the rostrum showing the dorsal penetration and divergence of the first upper incisor roots into the substance of the left and right premaxilla. Gray areas in the slices represent soft tissue. A digital rendering of the whole skull constructed from CT images in rostral view (**A**) is given as reference, indicating the approximate area covered by the slices (white frame). Scale = 1 mm. Abbreviations: **c** lower canine; **cI1** crown of first upper incisor; **i** lower incisors; **na** nasal; **nac** nasal cavity; **rI1** root of first upper incisor.

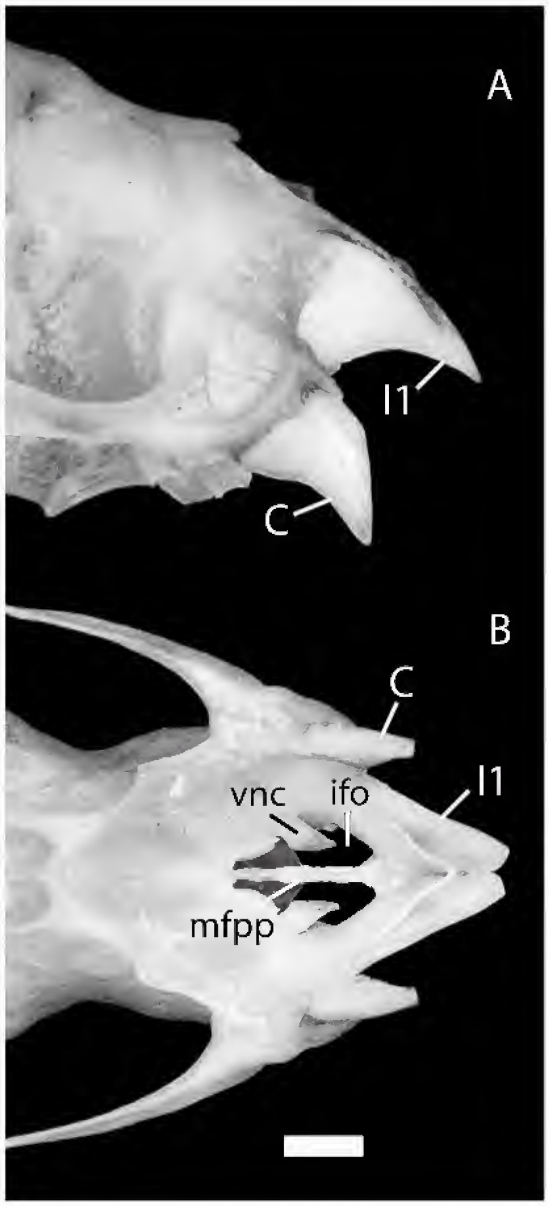


Fig. 21. *Desmodus rotundus* AMNH 248951, lateral (**A**) and ventral (**B**) view of the rostrum showing the dorsal displacement of the premaxilla with respect to the maxilla in (**A**) and the large size of the incisive foramina in (**B**). Scale = 1 mm. Abbreviations: **C** upper canine; **I1** first upper incisor; **ifo** incisive foramen; **mfpp** medial flange of the palatine process of the premaxilla; **vnc** ventral nasal concha or maxilloturbinate.

a wide lateral flange. The left and right medial flanges converge medially in an elevated position with respect to the alveolar line, forming a platform that receives the incisive incisure of the vomer dorsally.

The precise contacts of the nasal process are unclear, as the maxilloincisive and nasoincisive sutures are seamlessly fused in the specimens available to us (AMNH 257130, USNM 449282). The same is true for other yangochiropteran groups. The rostral edge of the nasal process is straight and gently inclined dorsocaudally so the external nasal aperture is sloping.

THYROPTERIDAE: The premaxilla in *Thyroptera* is likely complete and similar in most respects to the myzopodid premaxilla except for the fact that those incisive foramina are closed or, at least, greatly reduced. In *T. tricolor* AMNH 246236, a minute foramen is present on the left side, which possibly represents the corresponding incisive foramen of other bats like *Myzopoda*, whereas a right foramen is absent. An alternative interpretation of the thyropteran premaxilla is that the palatine process is absent altogether, so the rostral gap is similar to the emarginate condition seen in vespertilionids (see later). We favor the first option (palatine process present, incisive foramina obliterated) on the basis of comparisons with *Myzopoda* (see earlier), *Furipterus*, and *Natalus* (see later).

The rostral edge of the nasal process is gently slanted, as in *Myzopoda*. Sutures fuse early in the life of individuals, so the contacts of the nasal process are unclear. A precanine chamber, likely a glandular premaxillary sinus, is visible through the external nasal aperture, to which the premaxilla and probably the maxilla contribute (see Natalidae). Two bi-lobed incisors are obliquely inserted in the body; I1 is smaller than I2. The left and right bodies are separated by a wedge-shaped gap, as in *Myzopoda*.

FURIPTERIDAE: The premaxilla in the monotypic *Furipterus* is rather similar to the myzopodid premaxilla—that is, left and right bodies are well separated by a wedge-shaped gap, and the bodies connect with the medial flange of the palatine process via a thin bar. However, in *Furipterus* (e.g., *F. horrens* AMNH 265975, 267218), large incisive

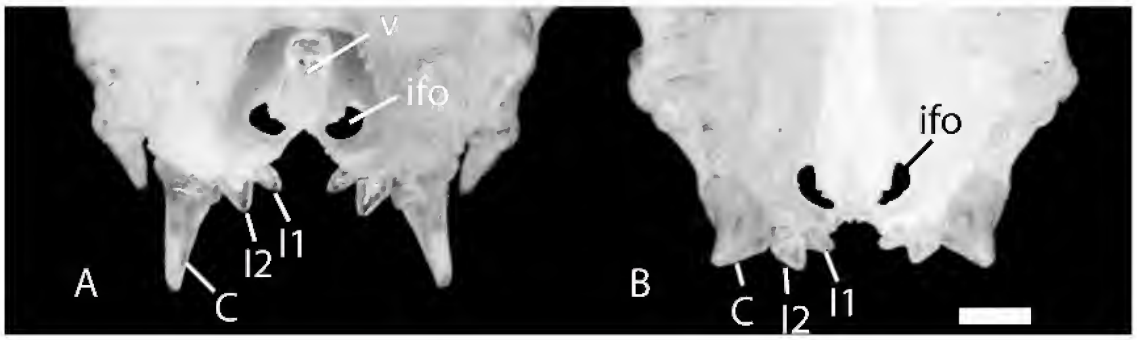


Fig. 22. *Myzopoda aurita* AMNH 257130, rostrodorsal (**A**) and caudoventral (**B**) view of the rostrum showing the wedge-shaped gap between the incisive foramina. Scale = 1 mm. Abbreviations: **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **v** vomer.

foramina pierce the palatine process, and upper incisors are subequal, relatively small, with a diastema separating I2 from the upper canine. The rostral shortening of the nasal creates a notch in the sloping dorsal edge of the premaxilla.

The other genus of the family, the monotypic *Amorphochilus* (e.g., AMNH 36261), is further modified. The left and right bodies are completely separated, apparently due to the lack of ossification of the medial flange of the palatine process. Incisive notches are large, widely open rostrally as a consequence of the absence of the thin bony bridge between the medial palatine process and the body, and separated from each other by the incisive incisure of the vomer. (It is unclear whether a reduced medial flange of the palatine process underlies the protruding vomer.)

NATALIDAE: The natalid premaxilla is similar to the myzopodid premaxilla in most respects, except that in natalids the premaxilla does not project as far rostrally, and the medial flange of the palatine processes is not elevated above the alveolar line. The straight lower canine fits in an arched socket formed by the diastema present between I2 and the upper canine. Early fusion precludes precise determination of the relationships of the nasal process of the premaxilla to the maxilla and nasals and makes it difficult to determine the precise location of the maxilloincisive suture. The thinness of the bone suggests that the premaxilla may participate, together with the maxilla, in a large precanine sinus (as seen in CT-scanned specimens; fig. 23; e.g., AMNH 206695). This character is shared with *Thyroptera*.

VESPERTILIONIDAE: This speciose family is remarkably uniform in premaxillary morphology. The nasal processes are fused to the maxilla in all taxa we examined. Observations of young specimens (e.g., *Lasiurus intermedius* AMNH 253710) indicate that the nasal processes articulate with the nasals dorsally (fig. 24). The left and right bodies are fused to the maxilla laterally at the level of the alveolar line and are separated from each other by a wide medial gap. This, together with the lack of palatine processes and the retracted anterior edge of the maxilla, contributes to the palatal emargination typical of vespertilionids (see Simmons and Geisler, 1998: characters 13–14). This emargination varies from very wide (e.g., in *Nyctalus* and *Lasiurus*, in which the emargination hollows virtually all the space between left and right tooth rows and reaches M1 caudally; fig. 25) to relatively narrow (e.g., in *Harpiocephalus*, in which the emargination is less wide than the space between the inner upper incisors [I1] and barely surpasses the canine caudally). The single important, variable feature that involves the body in vespertilionids is that it may bear one or two incisors.

MOLOSSIDAE: The nasal process of the premaxilla is always present and is fused to the maxilla in molossids. While *Cheiromeles* (fig. 26B) and some *Chaerephon* show small paired incisive foramina and a variously developed medial flange of the palatine process, variation exists regarding the body and the

Fig. 23. *Natalus stramineus* AMNH 206695, digital rendering constructed from CT images, lateral view of the skull. The thinness of the premaxillary bone makes visible a large precanine sinus indicated with (*). Scale = 5 mm.

palatine process in the remainder of the molossids. Molossid genera typically show "emarginate" or "non-emarginate" palates. Examples of the non-emarginate condition include *Cynomops*, *Eumops* (fig. 25A), *Molossops*, *Molossus*, *Promops* (New World) and *Cheiromeles* (fig. 26B), *Myopterus*, and *Mops* (Old World). In these forms, left and right premaxillary bodies are fused to each other, and incisive foramina may be present in the form of a single opening of varying size (e.g., in species of *Eumops*; fig. 26A).

In molossids that have emarginate palates (e.g., *Tadarida brasiliensis*; fig. 26C), the left and right bodies are separated by a small gap. This space is continued caudally in a narrow fissure in *Mormopterus*, *Nyctinomops*, and

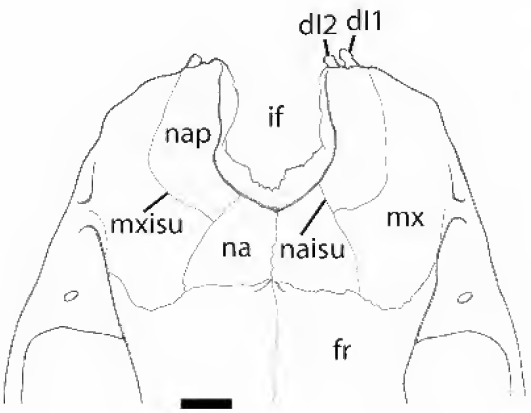


Fig. 24. *Lasiurus intermedius* AMNH 253710, line drawing of the dorsal view of the rostrum. Scale = 1 mm. Abbreviations: **bp** body of premaxilla; **fr** frontal; **if** incisive fissure; **mx** maxilla; **mxisu** maxilloincisive suture; **na** nasal; **naisu** nasoincisive suture.

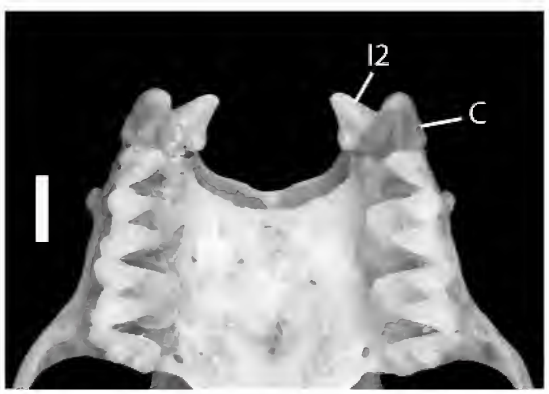
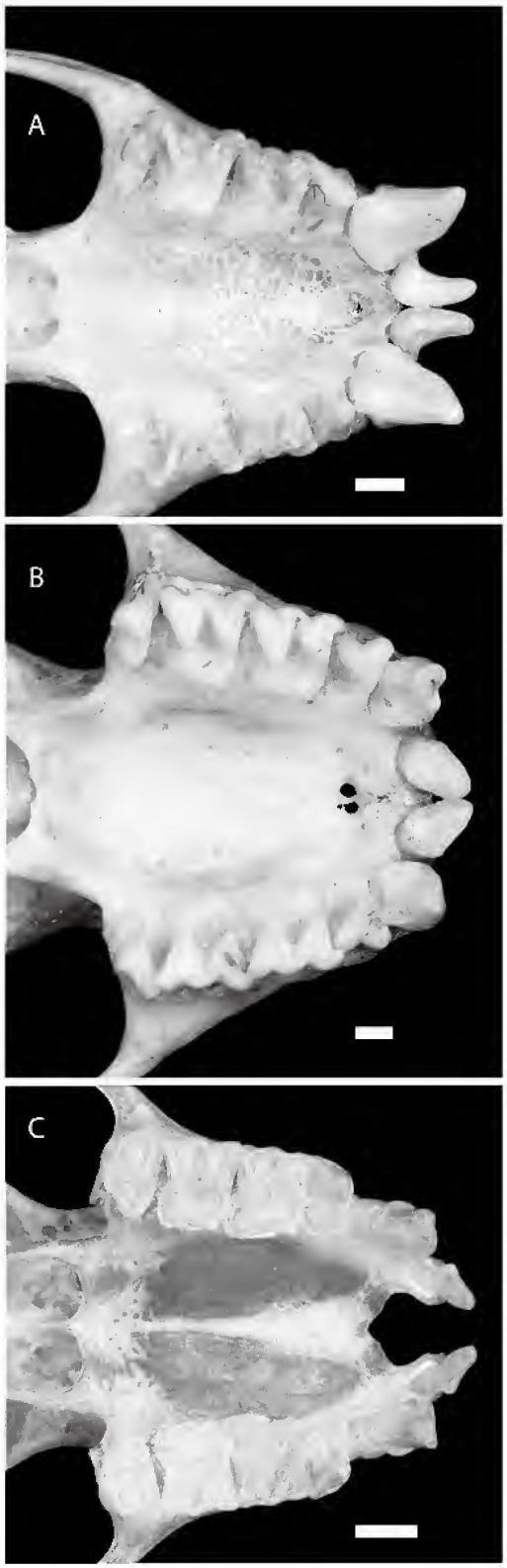


Fig. 25. *Lasiurus seminolus* AMNH 219950, ventral view of the anterior hard palate. Scale = 1 mm. Abbreviations: **C** upper canine; **I2** second upper incisor.



Tadarida. This resembles the condition seen in vespertilionids, although in the latter the emargination is markedly wider. In *Chaerephon pumilus*, the left and right bodies are separated by a gap, but each one is connected by a thin bar of bone to the medial flange of the palatine process, and paired incisive foramina are present (see Bouchard, 1998: fig. 2). However, in other species (e.g., *C. chapini*) the rostral gap is nearly closed, and the incisive foramina are minute (see Fenton and Eger, 2002: fig. 2), and yet in *C. ansorgei* the palatine process is not ossified (see Bouchard, 2001: fig. 2). In *Tomopeas ravus* (e.g., LSU 25072, 25084), formerly included in Vespertilionidae and transferred to Molossidae by Sudman et al. (1994; see also Simmons, 1998; Simmons and Geisler, 1998; and Gunnell and Simmons, 2005), the morphology of the premaxilla is as in typical vespertilionids.

In view of these morphologies, it is possible that the non-emarginate condition, with a single or no incisive opening, may represent a gradual secondary closing of an emarginate palate, as seen in vespertilionids and *Tomopeas*—successive sister groups to crown-group molossids (Simmons, 1998; Simmons and Geisler, 1998), as well as in *Tadarida* and related genera. That is, it is possible that the single palatine opening in molossids (e.g., in *Eumops*) would be primarily homologous to the medial accessory palatine foramen in other yangochiropterans (e.g., phyllostomids). This hypothesis can be tested with the histological study of the contents of the accessory palatine foramen.

EOCENE BATS: Simmons and Geisler (1998) described the basic structure of the premaxilla in the four best-known Eocene fossil genera of bats: *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. All of these taxa have a premaxilla with a well-developed nasal process that articulates with the maxilla via sutures. No notch is present between the premaxilla and maxilla anterior to the upper

←

Fig. 26. *Eumops perotis* AMNH 248390 (**A**), *Cheiromeles torquatus* AMNH 103922 (**B**), and *Tadarida brasiliensis* AMNH 219336 (**C**), ventral view of palate (see the text). Scale = 1 mm.

canine. In *Hassianycteris*, the only taxon known from multiple skulls preserved in lateral view, the nasoincisive suture is of intermediate length, and the premaxilla does not widen dorsally (Smith and Storch, 1981). There is no evidence of twisting of the medial edge of the premaxilla in any of the four Eocene genera.

The body of the premaxilla is clearly present and bears two incisors on each side of the jaw in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* (Simmons and Gesisler, 1998). The premaxilla appears to be orthoclivous in *Hassianycteris* (Smith and Storch, 1981); the degree of proclivity is unclear in the remaining Eocene genera.

Simmons and Geisler (1998) were unable to determine whether the palatine process was present or absent in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. However, Smith and Storch (1981: 158, 164) noted that *Hassianycteris* has a premaxilla in which "the palatal branch is not well developed; and the premaxillaries, although possibly in contact on the midline, do not appear to have been fused." They further noted that "the apparent shape and reduction of the premaxillary is quite reminiscent of the derived condition of this cranial element in emballonurids."

The number of upper incisors in *Icaronycteris* could not be determined unambiguously in the original description, but at least one incisor was present (Jepsen, 1966). Jepsen (1966) also noted presence of a medial diastema between the upper incisors in *Icaronycteris*, but it was not clear whether this was an artifact of preservation of the holotype. The palatine process was thought to be present in *Icaronycteris* (Simmons and Geisler, 1998), but details of morphology (e.g., presence or absence of medial and lateral flanges) could not be determined, because the lower jaws obscured the palate on all available specimens. A new specimen of *Icaronycteris* (AMNH 125000), in which the palate is exposed, clearly confirms the presence of a palatine process with a medial flange fully separating left and right incisive foramina, as well as a medial diastema between upper incisors (fig. 27). It also suggests that the adult number of upper incisors is two.

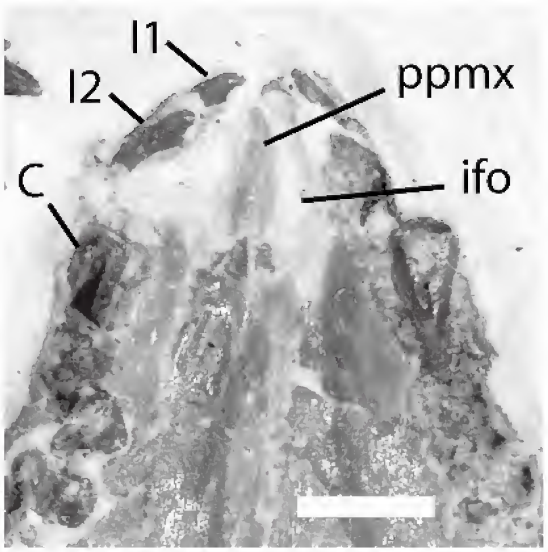


Fig. 27. *Icaronycteris* sp. AMNH 125000, ventral view of palate. Scale = 1 mm. Abbreviations: **C** upper canine; **I1** first upper incisor; **I2** second upper incisor; **ifo** incisive foramen; **ppmx** palatine process of premaxilla.

Characters of the Chiropteran Premaxilla

Character 1: *Premaxillary body absent (0); or body greatly reduced medially, not bearing teeth (1); or body reduced, bearing teeth, left and right counterparts separated by a space in the midsagittal line (2); or body well developed, left and right premaxillary bodies in contact medially, but partially separated by a notch (3); or left and right bodies well developed, in full contact medially, sutured (4); or left and right bodies well developed and fused medially (5).* The premaxillary body is entirely absent in three megadermatid genera (*Lavia*, *Macroderma*, and *Megaderma*; state 0). The megadermatid *Cardioderma* possesses an extremely reduced body without incisors (state 1; fig. 9). Most bats conserve a tooth-bearing premaxillary body that varies across taxa in the degree of medial development, ranging from widely separated left and right bodies (state 2) to fused left and right bodies (state 5). The range of observed variation suggests that this character should be treated as additive, reflecting a progressive pattern of body development associated with medial expansion, contact, and subsequent fusion of right and left counterparts. Our treatment of this feature

is modified from character 78 of Giannini and Simmons (2005), which was proposed in the context of Pteropodidae. Here we incorporate additional variation observed in microchiropterans (states 0–2 of the current character).

Character 2: *Nasal process of the premaxilla well developed, fused to the rostral process of the maxilla (0); or nasal process well developed, articulates with the maxilla via a foliate suture (1); or nasal process caudally reduced, attached to the maxilla via ligaments (2); or nasal process reduced to a splint of bone, attached to the maxilla via ligaments (3); or nasal process absent (4).* The degree of development of the nasal process and the type of articulation uniting the premaxilla and maxilla may be considered to be separate features, but they are intimately associated, and we therefore prefer to treat them as a single multistate character.

In their character 10, Simmons and Geisler (1998) coded the absence or reduction of the nasal process (state 1) versus its presence (state 0). In contrast, we prefer to describe the comparative reduction of the bone by defining more distinct states and incorporated information on the condition of the joint. The condition of the joint was partly coded in character 9 of Simmons and Geisler (1998). Our state 0 is defined similarly to, and is taxonomically distributed identically to, state 1 of character 9 in Simmons and Geisler (1998) and is equivalent to character 1 in Simmons and Conway (2001), except that in Simmons and Geisler (1998), character 9 refers to the premaxilla as a whole. Our state 1 corresponds to state 0 in character 9 of Simmons and Geisler (1998).

A major difference exists in both the interpretation and taxonomic distribution of state 2 of character 9 in Simmons and Geisler (1998), which coded the "movable" joint (i.e., a syndesmosis) present in all yinochiropteran families. Based on our observations, two types of syndesmoses instead of one are represented in bats, and their distribution among bat lineage does not overlap. In one type, the nasal process of the premaxilla articulates with the maxilla via a syndesmosis (coded in states 2 and 3 of the current character); this condition is seen in rhinopomatids, craseonycterids, emballonurids, and one megadermatid (*Cardioderma*). The remainder of yinochiropterans (rhinolophids and hipposiderids) lack a nasal process. In the second type of "movable" premaxilla, the palatine process (not present in all yinochiropterans) forms the syndesmosis; this condition is treated in character 3 (see later).

Character 3: *Palatine process of the premaxilla complete with medial and lateral flanges forming paired incisive foramina limited caudally by the maxilla (0); or palatine process complete, incisive foramina closed by a process of the maxilla (1); or medial flange absent, lateral flange present, the latter limiting a narrow incisive fissure (2); or lateral flange absent, paired incisive foramina partially or totally embedded in bar-like medial flanges attached caudally to the maxilla via a syndesmosis (3); or medial flange absent, lateral flange attached laterally to the maxilla via a syndesmosis and surrounding a pear-shaped incisive fissure (4); or both lateral and medial flanges absent, wide incisive fissure (5).*

This character combines a coding of the premaxillary contribution to the hard palate (from the lateral flanges, medial flanges, both, or none) with the degree of development of the incisive fissure/foramina, as these two features are intimately associated. Based on *Pteropus*, the incisive foramen/fissure transmits the nasopalatine duct and nasopalatine nerve but no major vessel (Giannini et al., 2006).

State 0 represents the typical condition of most mammals (paired incisive foramina), which is present in many yangochiropteran bats (e.g., *Artibeus*, *Natalus*, *Pteronotus*, *Thyroptera*). In *Noctilio*, the incisive foramina are closed by a process of the maxilla (state 1). State 2 is typical of some molossids (e.g., *Nyctinomops*, *Tadarida*, *Tomopeas*). State 3 is the condition found in hipposiderids and rhinolophids (see family accounts). State 4 is an autapomorphy of Nycteridae. Finally, a large incisive fissure, which is a consequence of the absence of any premaxillary contribution to the hard palate (state 5), is typically present in Pteropodidae as well as in many microbats—for example, vespertilionids, emballonurids, rhinopomatids, and craseonycterids. In vespertilionids, the incisive fissure is rostrally open due to the medially reduced premaxillary bodies and is caudally wide due

to a retracted rostral edge of the palatine process of the maxilla. Unlike the previous character, a simple transformation series cannot be construed among the states defined here, so we treat this character as unordered to avoid an assumption-laden character reconstruction.

Part of the variation described here was coded in two characters scored in mormoopids by Simmons and Conway (2001). Specifically, their character 2 scored the absence/presence of a palatine process as a whole, and their character 3 coded the absence/presence of incisive foramina.

Character 4: *Premaxillary body thin (0); or of intermediate thickness (1); or deep (2)*. A traditional character in megachiropteran systematics, this character was used as an ordered phylogenetic character by Giannini and Simmons (2005: character 79). Most megachiropterans show a body of intermediate depth, in which the body is slightly deeper than the length of the incisor roots (state 1). In *Dobsonia*, macroglossines, and myonycterines, the body is reduced in depth and barely holds the incisor roots (state 0). Nyctimenines and *Megaerops ecaudatus* show a deep body that extends well beyond the incisor roots and gives the rostrum an elevated aspect. The variation in microbats has not been analyzed in the literature, although this character definition fits the variation across microbats (table 1). The premaxillary body is thin in rhinolophids, hipposiderids, nycterids, *Craseonycteris*, and *Anoura*, as well as in other nectar-feeding phyllostomids and in the majority of mormoopids, noctilionids, furipterids, thyropterids, myzopodids, natalids, molossids, and vespertilionids. The premaxillary body is of intermediate thickness in most phyllostomids and *Mystacina*. No microbat shows a thick body.

Character 5: *Dorsomedial process of the premaxilla absent (0); or present (1)*. The dorsomedial process of the premaxilla is unique to Scotonycterini, a group of epomophorine pteropodids composed of three species in two genera (*Casinycteris* and *Scotonycteris*; see Giannini and Simmons, 2005: character 83). This minute process (roughly 2 mm) arises bilaterally in the midsagittal plane from the dorsal edge of the premaxillary body into the external nasal aperture (fig. 5).

Character 6: *Interincisive crest absent (0); or present (1)*. The interincisive crest is a keel formed in the medial union of left and right palatine processes just dorsal to the interincisive suture. An interincisive crest is present among bats only in some hipposiderids (e.g., *Rhinonycteris*; state 1; fig. 12). This is character 1 of Bogdanowicz and Owen (1998) and character 10 of Hand and Kirsch (1998).

Character 7: *Ventrolateral margin of maxilloincisive suture lies in the same plane as the upper alveolar line (0); or lies above alveolar line, creating a notch between the premaxilla and maxilla in front of the upper canine (1)*. The vast majority of bats have a maxilloincisive suture whose ventrolateral margin lies in the same plane as the upper alveolar line. In megabats, state 1 occurs in *Pteropus* + *Acerodon* (fig. 4), in *Eidolon*, and in *Eonycteris* (Pteropodidae; Giannini and Simmons, 2005: character 85). In microbats, a notch between premaxilla and maxilla appears in *Craseonycteris*, *Noctilio*, and *Natalus*, although it is less marked than in megabats.

Character 8: *Nasoincisive suture long, nasal-premaxilla contact broad (0); or contact of intermediate breadth (1); or point contact (2); or no contact present, nasal process does not reach the nasal (3)*. Variation in the length of the nasoincisive suture characterizes a number of bat lineages. Our treatment of this character is based on character 81 of Giannini and Simmons (2005). Dunlop (1998) treated this variation to some extent in two characters, one (her character 80) in which contact between the nasal process of the premaxilla and the nasal was scored as a presence/absence character. In the other, Dunlop (1998: character 83) included proximal (i.e., dorsal) widening of the premaxilla in a complex describing the unique pad-like dorsal flange seen in some emballonurids (see next character and Emballonuridae). Our character reflects specifically the dorsal development of the nasal process and the corresponding variation in the nasoincisive suture (see Pteropodidae), so it is not applicable in taxa in which the nasal process is missing altogether (state 4 of character 2) or is reduced to a splint of bone (state 3 of character 2). Because of the

seemingly progressive nature of the transformations described in this character, it is probably best treated as an ordered character.

Character 9: *Nasal process without dorsal pad-like flange (0); or nasal process widens dorsally forming a pad-like flange (1).* This flange is unique to some emballonurids (e.g., *Rhynchonycteris*, *Saccopteryx*, *Taphozous*) and consists of a widening of the dorsal end of the nasal process both medially and caudally (fig. 6). As defined, the presence of the flange varies within Emballonuridae, and it corresponds to state 1 of character 83 in Dunlop (1998), which was also used by Lim et al. (2004: character 29; see discussion under Emballonuridae).

Character 10: *Left and right nasal processes not in contact dorsally (0); or fused in the midsagittal line to form a bridge over the external nasal aperture (1).* Fusion of the right and left nasal processes over the dorsum of the rostrum is an autapomorphy of *Craseonycteris* (see Craseonycteridae). It is possible that this condition is related to the dorsal widening of the nasal process seen in some emballonurids (state 1 of previous character) carried to an extreme. However, the condition in *Craseonycteris* is unique, involving also fusion of the left and right processes. We therefore treat these as separate characters.

Character 11: *Caudal edge of nasal process (lateral part of the maxilloincisive suture) caudally straight (0); or gently convex caudally (1); or caudally squared off (2).* The rostral portion of the maxilloincisive suture takes different forms in different bat taxa. It involves the trajectory of the lateral portion of the maxilloincisive suture, which can take different shapes, from straight to rostrally concave to angled, so that a caudally directed vertex is formed (fig. 4). As defined, this character is a combination of character 81 of Dunlop (1998, including states 0 and 1 and scored in emballonurids) and character 82 of Giannini and Simmons (2005, including states 1 and 2 and scored in Pteropodidae). State 0 is seen in some emballonurids (e.g., some *Diclidurus*, *Cittarops*; Dunlop, 1998). State 1 probably is the norm in most bats, including most emballonurids (e.g., *Cormura*, *Emballonura*, *Mosia*, *Rhynchonycteris*, *Saccopteryx*, some *Taphozous*) and most pteropodids (e.g., *Cynopterus*, *Epomophorus*, *Macroglossus*, *Nyctimene*, *Rousettus*). A squared caudal edge of nasal process (state 2) is present in pteropodine megabats (e.g., *Acerodon*, *Pteropus*; Giannini and Simmons, 2005). This character was considered ordered.

Character 12: *Nasal process without lateral expansions (0); or with lateral expansions (1).* Andersen (1912) noted the lateral expansion of the external nasal aperture (i.e., in the nasal process of the premaxilla) in *Nyctimene*, a trait that Giannini and Simmons (2005) coded in their character 86. A laterally expanded nasal process also characterizes the closely related *Paranyctimene*. Among microbats, we noted a similar condition only in Mystacinidae and Noctilionidae. All other bats we examined have a nasal process that lacks lateral expansions.

Character 13: *Medial accessory palatine foramen absent (0); or present (1).* A single medial foramen in the substance of the palatine aspect of the premaxilla occurs in some noctilionoid bats (e.g., *Anoura*, *Myzopoda*, *Pteronotus*). As pointed out earlier, the presence of this foramen (state 1) may be a consequence of a secondary closing of the wedge-shaped gap that partially separates the left and right premaxillary bodies in some microbats (state 1 in previous character).

Character 14: *Premaxilla proclivous, extending anteriorly beyond the level of the upper canine root (0); or premaxilla orthoclivous, terminates at the level of the upper canine root (1).* While in all yinochiropteran bats and some pteropodids (e.g., *Cynopterus*, *Nyctimene*) the premaxilla does not project rostrally beyond the level of the upper canine (state 1), it does so in most yangochiropterans, with the exception of vampire bats (Phyllostomidae: Desmodontinae) and *Myzopoda*, as well as in many pteropodids (e.g., *Pteropus*, *Rousettus*).

Character 15: *Medial edge of premaxilla nearly straight (0); or twisted (1).* In most bats in which the nasal process is present, the medial edge of the premaxilla is only slightly curved, if at all (state 0). The premaxilla of some emballonurids shows this condition (*Balantiopteryx*, *Diclidurus ingens*,

Emballonura raffrayana, *E. monticola*, *E. furax*, *E. beccarii*, and *Mosia*; Dunlop, 1998). In the remainder of emballonurids, "the medial edge can twist so that the premaxilla is proximally dorsoventrally flattened and distally lateromedially flattened" (Dunlop, 1998: 80; state 1). Dunlop (1998) and Lim et al. (2004) coded this variation in their characters 82 and 28, respectively.

Character 16: *Precanine premaxillary sinus absent (0); or present (1)*. In *Thyroptera* and *Natalus*, the premaxilla forms a concave sinus that opens medially into the nasal cavity (specifically, the *meatus nasi communis*) in front of the upper canine. This sinus is delimited caudally by a thin, vertical wall of bone probably related to the conchal crest and the maxilloturbinate or ventral nasal concha. Externally this sinus is visible in CT-scanned specimens because of the thinness of the premaxillary bone (fig. 23). The content of this sinus is unknown to us, and its occurrence in bats other than *Thyroptera* and *Natalus*, in which it is most evident, remains to be investigated.

Phylogenetic Patterns

Mapping

Character 1: Mapping character 1 onto the morphological tree reveals that, in spite of the missing scoring of Eocene bats, the ancestral chiropteran is unambiguously assigned state 4 (body well developed and left and right bodies sutured), which is the generalized mammalian condition (fig. 28). In turn, the crown microchiropteran group is assigned state 3 (left and right bodies partially separated by notch) if the character is treated as ordered. If unordered, this node and the next nodes up in the tree are ambiguously optimized as either 2 or 3 (nodes marked * in fig. 28)—that is, left and right bodies either separated or in contact but partially separated by a notch. Within the microbat crown group, two trends are apparent. First, parallel body reduction or loss seems to have occurred, twice in Yinochiroptera (state 2 → 1 in Emballonuridae and 2 → 0 or 1 in Megadermatidae) and again in the ancestor of Molossidae + Vespertilionidae. Second, a trend to premaxillary body strengthening via joint fusion (state 3 → 5) occurred in Noctilionoidea. Other details are shown in figure 28.

In the DNA tree (fig. 29), the ancestral state for bats is ambiguous (either state 3 or 4). The DNA tree requires 50% (if unordered) to 100% (if ordered) additional extra steps in the evolution of the premaxilla than required by topology of the morphological tree (table 1). Mapping character 1 onto the DNA topology provides synapomorphies of Yangochiroptera sensu Teeling et al. (2000; state 3) and of Megachiroptera (state 4), but either state may have appeared earlier, given ambiguities along the backbone of the chiropteran tree. Trends toward strengthening and weakening of the premaxilla appear scattered across the DNA tree as compared with the morphological topology.

Character 2: The morphological tree of Gunnell and Simmons (2005) requires only two (if ordered) or one (if unordered) extra steps in this character (fig. 30). This difference is due only to the 2 → 4 transformation inferred at the node that defined Rhinolophoidea sensu Simmons and Geisler (1998; i.e., containing nycterids, rhinolophids, hipposiderids, and megadermatids), which costs one step if the present character is treated as non-additive and two steps if it is treated as additive. The ancestral bat is assigned state 1—that is, a well-developed premaxilla sutured to the maxilla—and this state is retained in all nodes up to the microchiropteran crown clade. In the crown clade, two opposite trends apparently developed: first, a weakening of the joint and the bone in Yinochiroptera, further reinforced by the loss of the nasal branch in Rhinolophoidea; and second, a strengthening of the bone by fusion of the nasal process to the maxilla, which is an unreversed synapomorphy of Yangochiroptera sensu Koopman (1985). Three times as many extra steps are required by the molecular topology (fig. 31) because three independent losses of the nasal process (once each in rhinolophids + hipposiderids, megadermatids, and nycterids) are required by that tree topology.

Character 3: In the morphological tree, the present character requires just one extra step. The ancestral chiropteran node is assigned state 0—that is, a complete, sutured palatine process with paired incisive foramina (fig. 32).

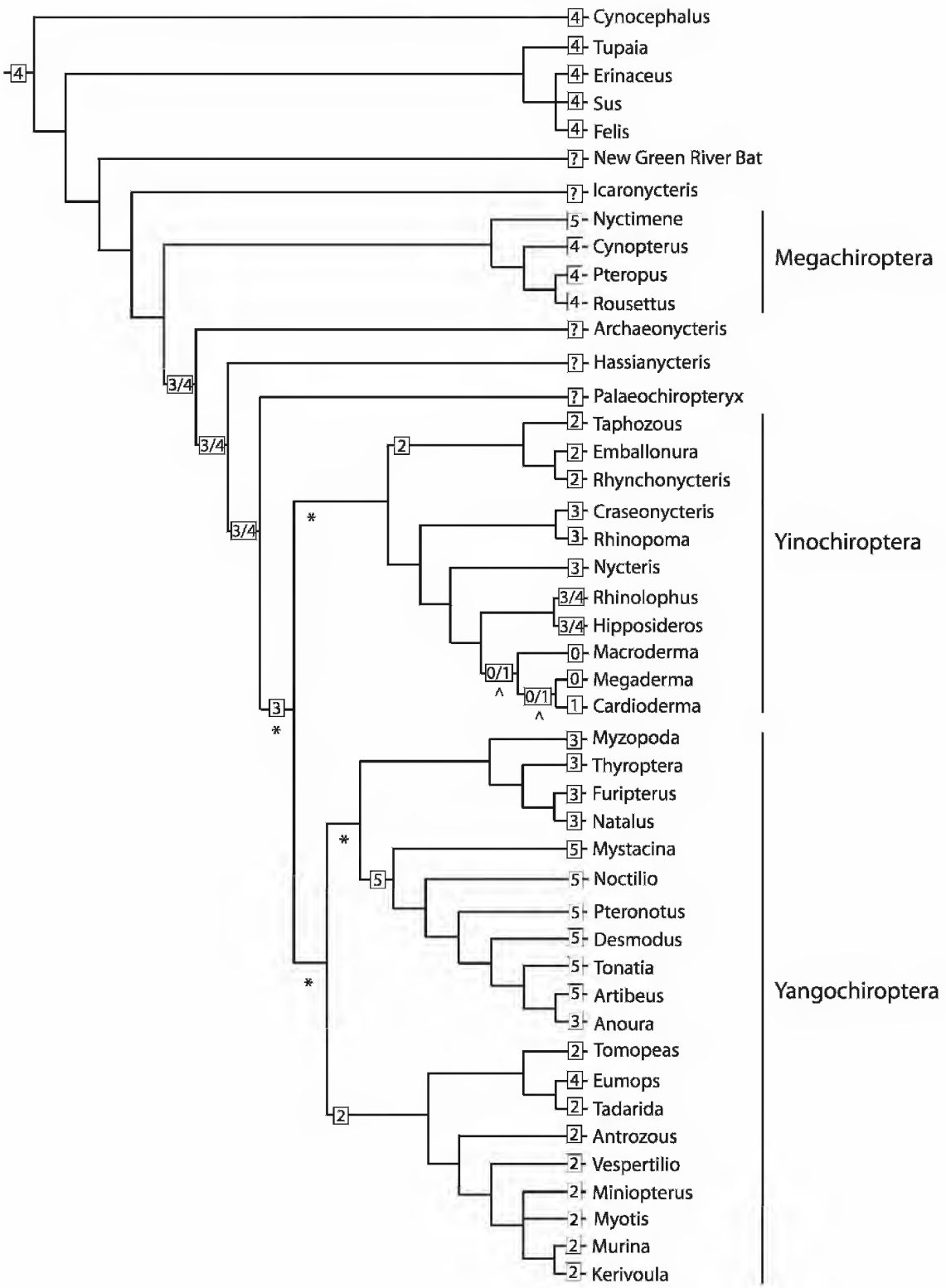


Fig. 28. Mapping of the first premaxillary character, body of the premaxilla, onto the morphology tree of Gunnell and Simmons (2005). See the text for definition of character states. If the character is unordered, nodes marked * become umbiguous and nodes marked ∧ are assigned state 0.

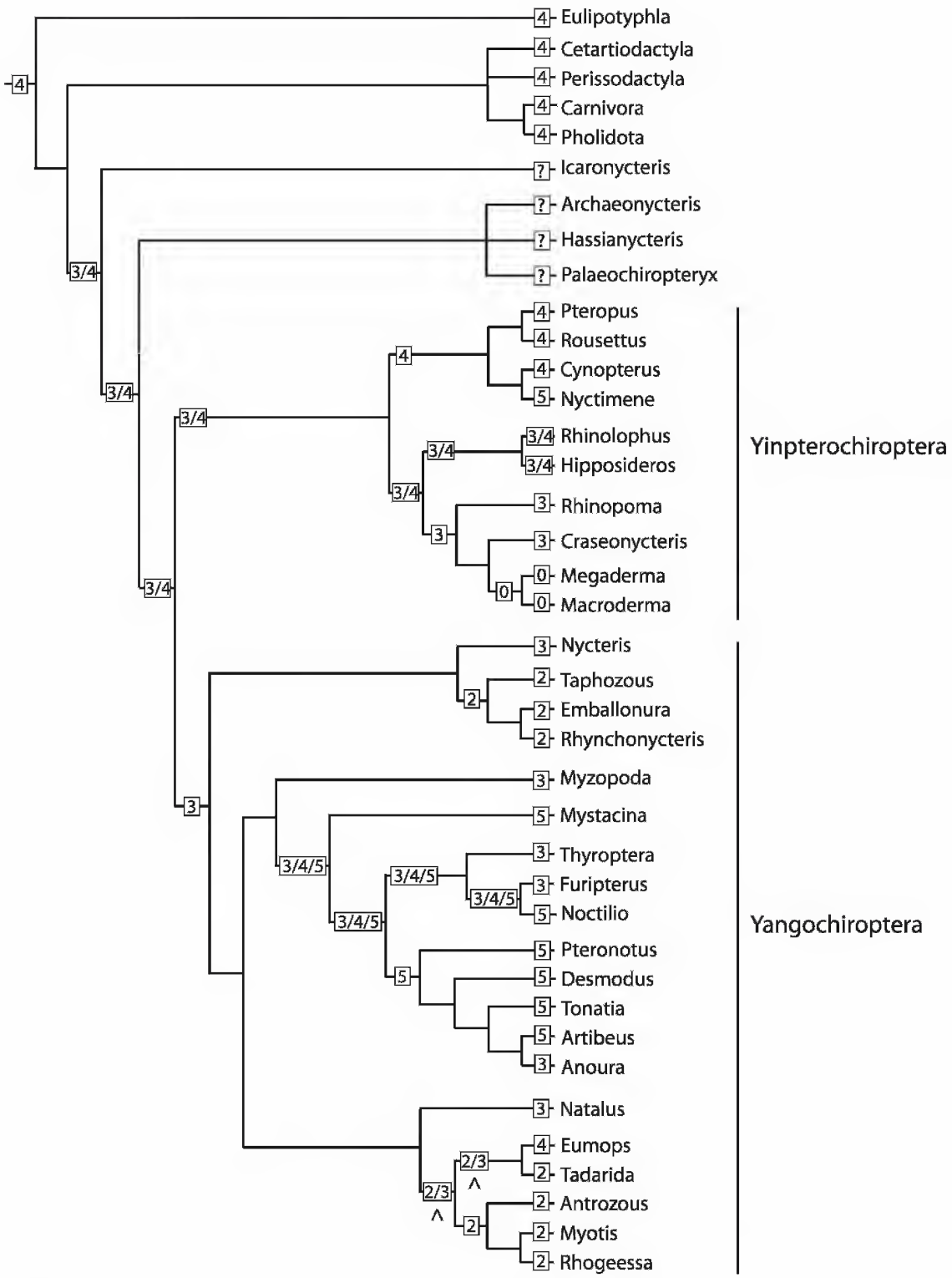


Fig. 29. Mapping of the first premaxillary character, body of the premaxilla (ordered) onto the DNA tree of Teeling et al. (2005). See the text for definition of character states. If the character is unordered, nodes marked ∧ are assigned state 2.

TABLE 1

Scorings of 16 Premaxillary Characters Described Herein Across Selected Outgroups (those used by Teeling et al., 2005) and Bat Terminals (see text)

Characters 5, 6, and 10 are uninformative for this taxonomic sampling (character 5, state 1, occurs in Scotonycterini megachiropterans; not included). Inapplicable and missing character states are indicated (-) and (?), respectively.

Groups/families	Terminals	Characters															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroups[a]																	
Eulipotyphla	*Condylura|Scalops|Talpa*	4	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0
Artiodactyla	*Bos|Tragelaphus*	4	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0
Perissodactyla	*Equus|Ceratotherium*	4	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0
Carnivora	*Felis|Panthera*	4	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0
Pholidota	*Manis*	4	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Ingroup																	
Icaronycteridae[b]	*Icaronycteris*	4	1	0	?	0	0	0	1	0	0	1	0	0	0	0	0
Archaeonycteridae[b]	*Archaeonycteris*	?	1	?	?	0	?	0	?	?	0	?	?	?	?	0	0
Hassianycteridae[b]	*Hassianycteris*	?	1	?	?	0	?	0	?	?	0	?	?	?	?	0	0
Palaeochiropterygidae[b]	*Palaeochiropteryx*	?	1	?	?	0	?	0	?	?	0	?	?	?	?	0	0
Pteropodidae	*Pteropus*	4	1	5	1	0	0	1	1	0	0	2	0	-	0	0	0
	Rousettus	4	1	5	1	0	0	0	1	0	0	1	0	-	0	0	0
	Cynopterus	4	1	5	1	0	0	0	2	0	0	1	0	-	1	0	0
	Nyctimene	5	0	5	2	0	0	0	3	0	0	1	1	-	1	0	0
Rhinolophidae	*Rhinolophus*	2/3	4	3	0	0	0	-	-	-	-	-	-	0	1	0	0
Hipposideridae	*Hipposideridae*	2/3	4	3	0	0	0	-	-	-	-	-	-	0	1	0	0
Megadermatidae	*Megaderma*	0	4	5	-	-	-	-	-	-	-	-	-	-	-	0	0
	Macroderma	0	4	5	-	-	-	-	-	-	-	-	-	-	-	0	0
	Cardioderma	1	3	5	-	-	-	-	-	-	-	-	-	-	-	0	0
Craseonycteridae	*Craseonycteris*	3	2	5	0	0	-	1	1	0	1	1	0	0	1	0	0
Rhinopomatidae	*Rhinopoma*	3	2	5	1	0	-	0	3	0	0	1	0	-	1	0	0
Emballonuridae	*Emballonura*	2	2	5	0	-	-	0	1	0	0	1	0	-	1	1	0
	Rhynchonycteris	2	2	5	0	-	-	0	1	1	0	1	0	-	1	1	0
	Saccopteryx	2	2	5	0	-	-	0	1	1	0	1	0	-	1	1	0
	Taphozous	2	2	5	0	-	-	0	1	1	0	1	0	-	1	1	0
Nycteridae	*Nycteris*	3	4	4	0	0	0	0	-	-	-	-	-	0	1	0	0
Phyllostomidae	*Artibeus*	5	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0
	Macrotus	5	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0
	Anoura	3	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
	Tonatia	5	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
	Desmodus	5	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Mormoopidae	*Pteronotus*	5	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
	Mormoops	5	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0
Noctilionidae	*Noctilio*	5	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0
Furipteridae	*Furipterus*	3	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Thyropteridae	*Thyroptera*	3	0	0	0	0	0	0	?	0	0	1	0	0	0	0	1
Mystacinidae	*Mystacina*	5	0	0	1	0	0	0	2	0	0	1	1	1	0	0	0
Myzopodidae	*Myzopoda*	3	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0
Vespertilionidae	*Antrozous*	2	0	5	0	-	-	0	1	0	0	1	0	-	0	0	0
	Rhogeessa	2	0	5	0	-	-	0	1	0	0	1	0	-	0	0	0
	Myotis	2	0	5	0	-	-	0	1	0	0	1	0	-	0	0	0
Molossidae	*Tadarida*	2	0	2	0	-	0	0	1	0	0	1	0	-	0	0	0
	Eumops	4	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0
Natalidae	*Natalus*	3	0	0	0	0	0	1	?	0	0	1	0	0	0	0	1

[a]A series of laurasiatherian mammals used as outgroups in Teeling et al. (2005), in which each terminal was a chimeric taxon composed of the genera listed, except Pholidota, which was represented by a single genus (*Manis*).

[b]Eocene families.

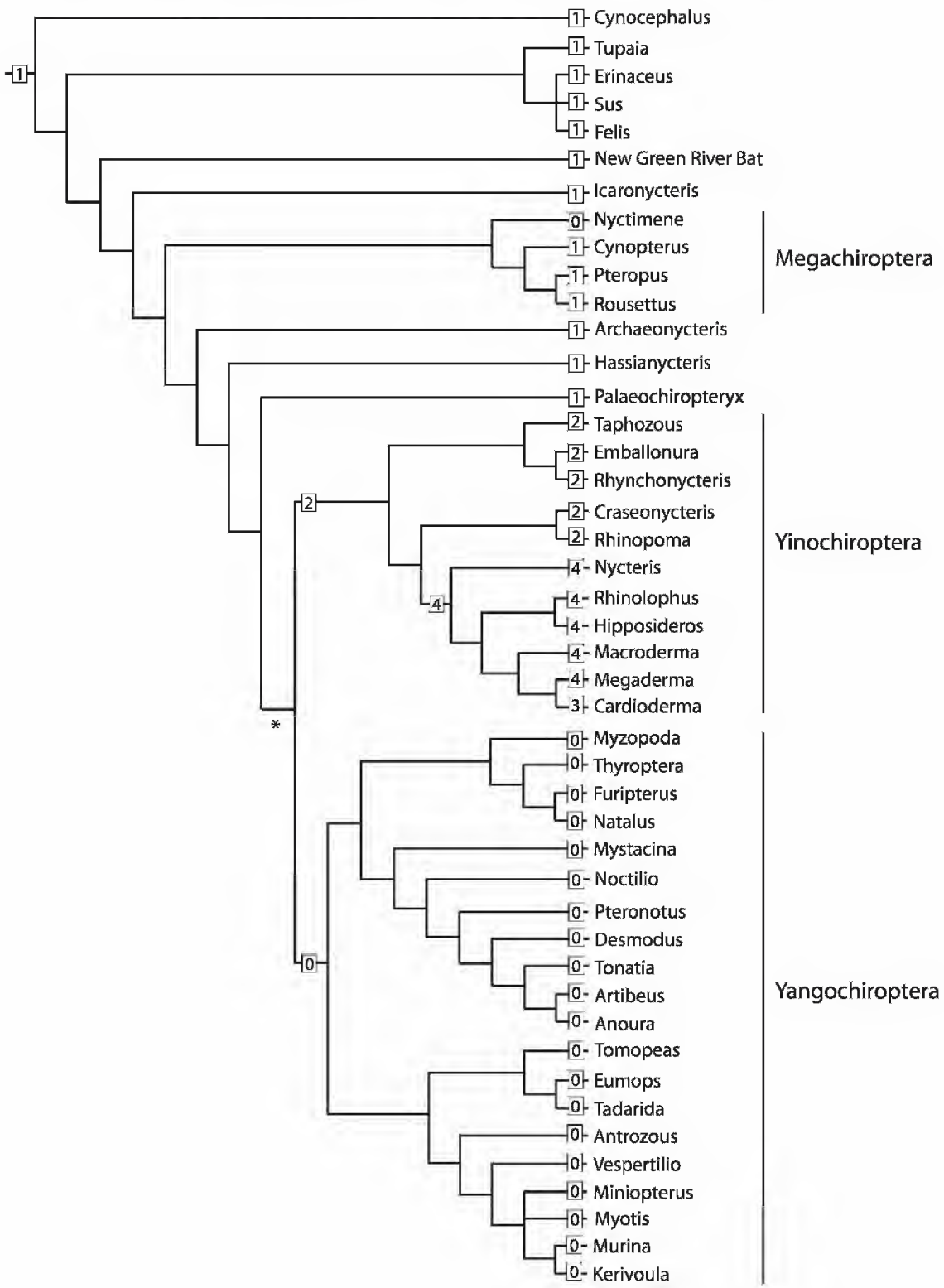


Fig. 30. Mapping of the second premaxillary character, nasal process of the premaxilla, onto the morphology tree of Gunnell and Simmons (2005). See the text for definition of character states. If unordered, the node marked * is ambiguous.

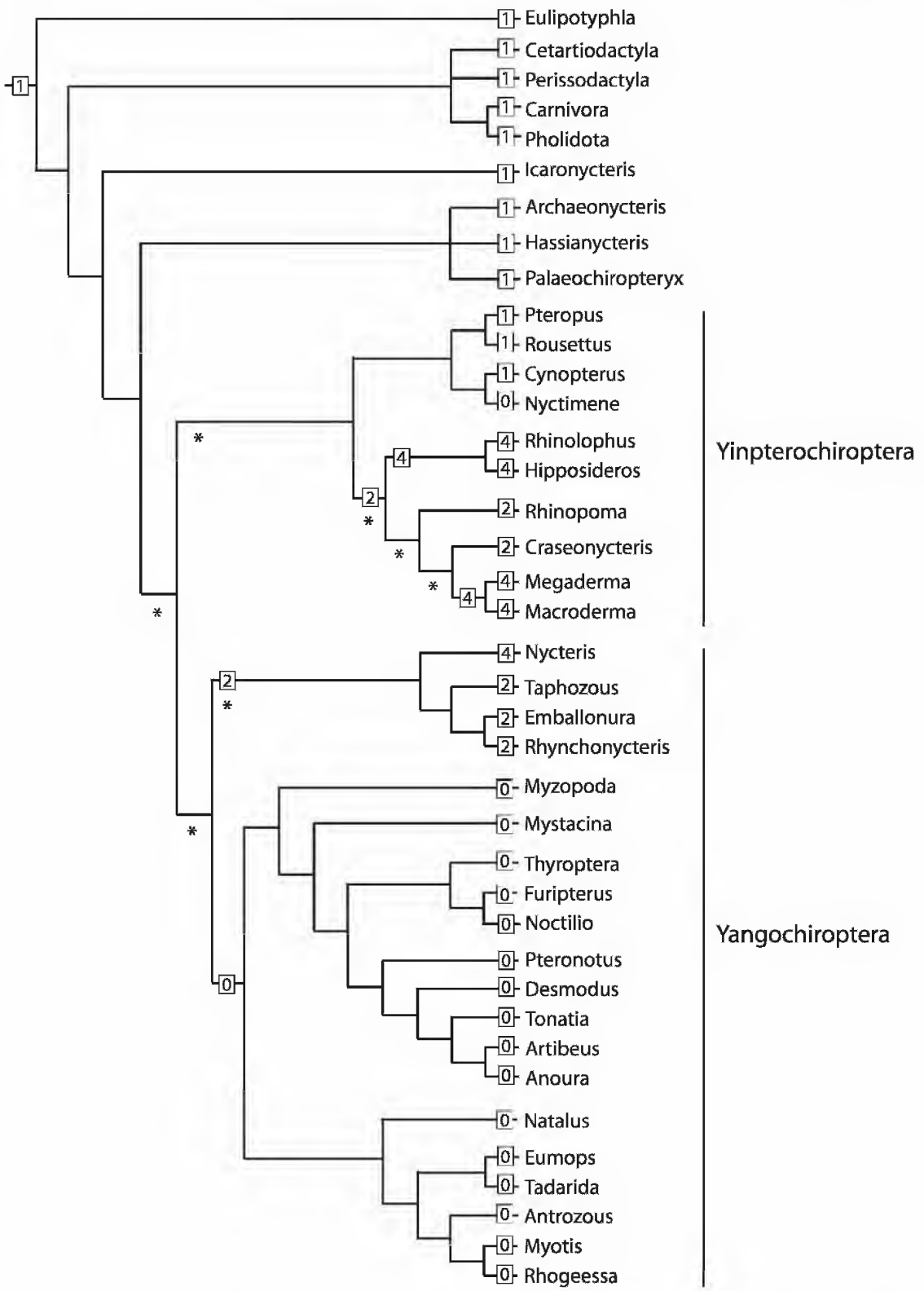


Fig. 31. Mapping of the second premaxillary character, nasal process of the premaxilla, onto the DNA tree of Teeling et al. (2005). See the text for definition of character states. If unordered, nodes marked * are ambiguous.

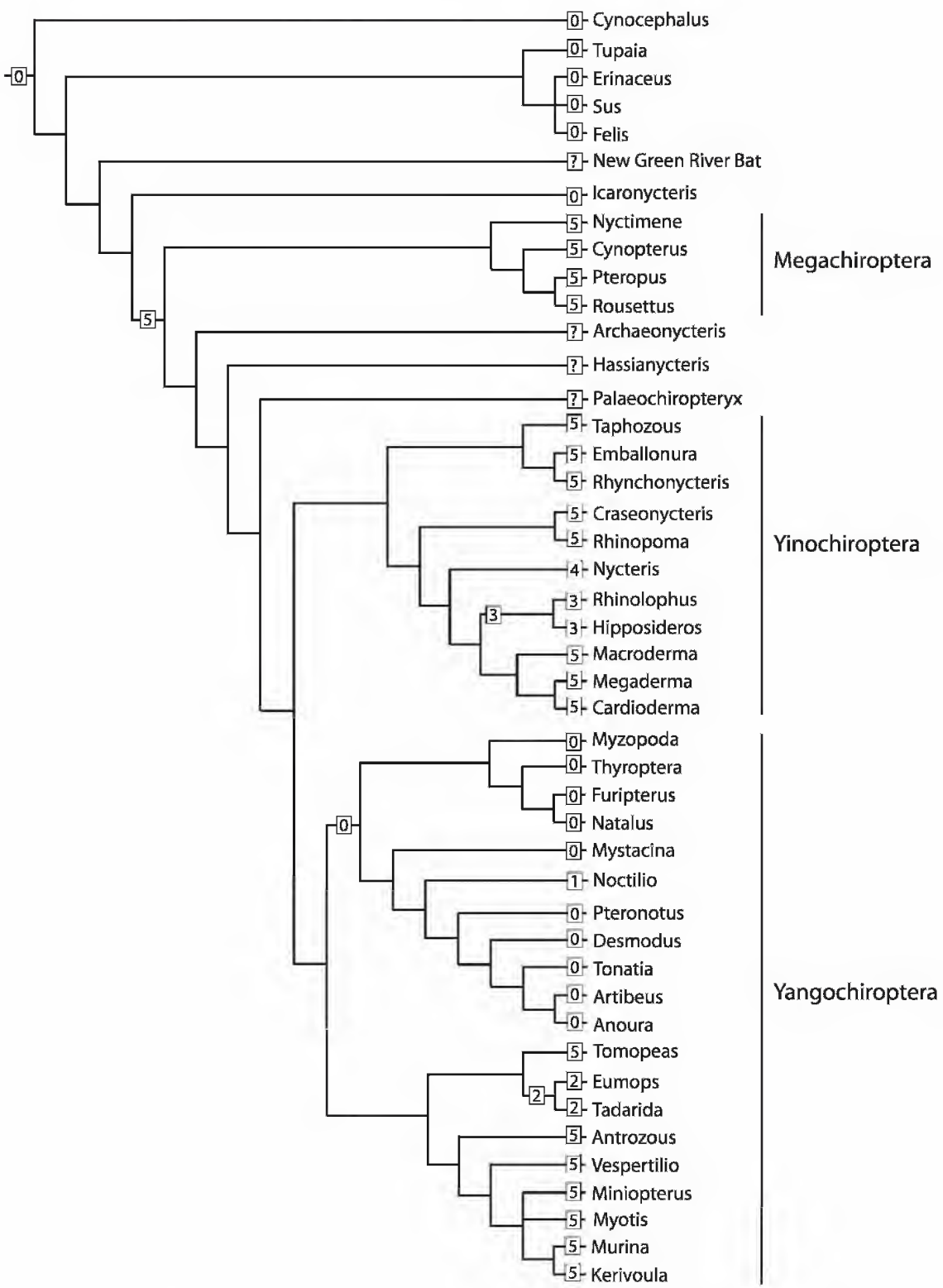


Fig. 32. Mapping of the second premaxillary character, palatine process of the premaxilla, onto the morphology tree of Gunnell and Simmons (2005). See the text for definition of character states.

The chiropteran crown clade is assigned state 5, which implies a failure in the ossification of the palatine flanges as compared with the ancestral condition. This simplified premaxilla with a wide incisive fissure (state 5) is modified in nycterids (state 5 → 4, reossification of the lateral flange with fixed ligament joint), in rhinolophids + hipposiderids (state 5 → 3, reossification of the medial flange with movable ligament joint), in (Nataloidea + (*Mystacina* + Noctilionoidea)) sensu Simmons and Geisler (1998; state 5 → 0, reossification of medial and lateral flange, with sutured joint), in molossids (state 5 → 2, reossification of the lateral flange, fused). Finally, in *Noctilio* (state 0 → 1) the incisive foramina are closed by the maxilla.

In the molecular tree (fig. 33) the ancestral chiropteran node is assigned state 0, as in the morphological tree, but most backbone nodes are ambiguously assigned states 0 or 5, which makes it extremely difficult to interpret the evolution of the palatine process of the premaxilla. Three extra steps are required by this topology, and just two of the changes listed earlier remain unambiguous in the molecular topology (the 5 → 3 change in rhinolophids + hipposiderids and the 0 → 1 change in *Noctilio*).

Tree Searches

Using the 16 premaxillary characters defined earlier, an equally weighted parsimony tree search resulted in an initial set of 160 optimal trees of 53 steps, and >10,000 trees of the same length after final swapping. The strict consensus of either the initial set or the total set of optimal trees has nine nodes resolved, all of which also appear in the implied-weights analysis of the same data (initial set of 340 trees at 4.57 unit of fit, 2,232 optimal trees after final swapping). The latter analysis recovered seven additional nodes, thus totaling 17 nodes in the strict consensus. In both analyses, *Nyctimene* and *Mystacina* appear as sister taxa. These two bats share similar scorings for premaxillary characters, so they are grouped together within a noctilionoid clade. Parsimony analyses without *Nyctimene* (fig. 34A) resulted in the same relationships among remaining taxa in each analysis type (equal weights analysis: initial set of 360 trees of 49 steps, final set of >10,000 equally optimal trees; implied weights analysis: initial set of 580 trees at 4.07 units of fit, final set of 2,232 of equally optimal trees). The best-resolved analysis without *Nyctimene* (implied weights) recovered the following groups: Yinochiroptera sensu Koopman (1985), Yangochiroptera sensu Koopman (1985), Rhinolophoidea sensu Simmons and Geisler (1998), the families Emballonuridae and Vespertilionidae, and a depauperate Noctilionoidea (excluding *Anoura*, *Thyroptera* and *Furipterus*).

Another approach to dealing with the nesting of *Nyctimene* within a non-pteropodid clade in the absence of other evidence is to use constrained searches. We fixed two groups (marked "C" in fig. 34B), Chiroptera and Pteropodidae, and performed parsimony analyses as specified. The equal-weights analysis resolved only two groups besides those constrained (Emballonuridae and an emballonurid grouping inclusive of *Rhynchonycteris*, *Saccopteryx* and *Taphozous*). The implied-weights analysis recovered eight additional groups, including Yinochiroptera, Rhinolophoidea, and the same reduced Noctilionoidea (fig. 34B).

Excluding fossils (and *Nyctimene*) from the analysis increased basal resolution under equal weights. In this analysis (final set of 171 trees of 49 steps), the remaining pteropodid genera (*Pteropus*, *Rousettus*, and *Cynopterus*) joined Yinochiroptera sensu Koopman (1985) in a clade resembling Yinpterochiroptera of Teeling et al. (2000), except for the inclusion of Emballonuridae and Nycteridae, which appear as sister taxa of Yangochiroptera sensu Koopman (1985) in the recent molecular studies (Teeling et al., 2000, 2005). The analysis under implied weights (final set of 35 trees of 4.07 units of fit) recovered seven additional nodes (fig. 35).

DISCUSSION

The premaxilla is variously reduced in bats as compared with other mammals (Wible and Novacek, 1988), and, as we have shown, reductions (and other modifications)

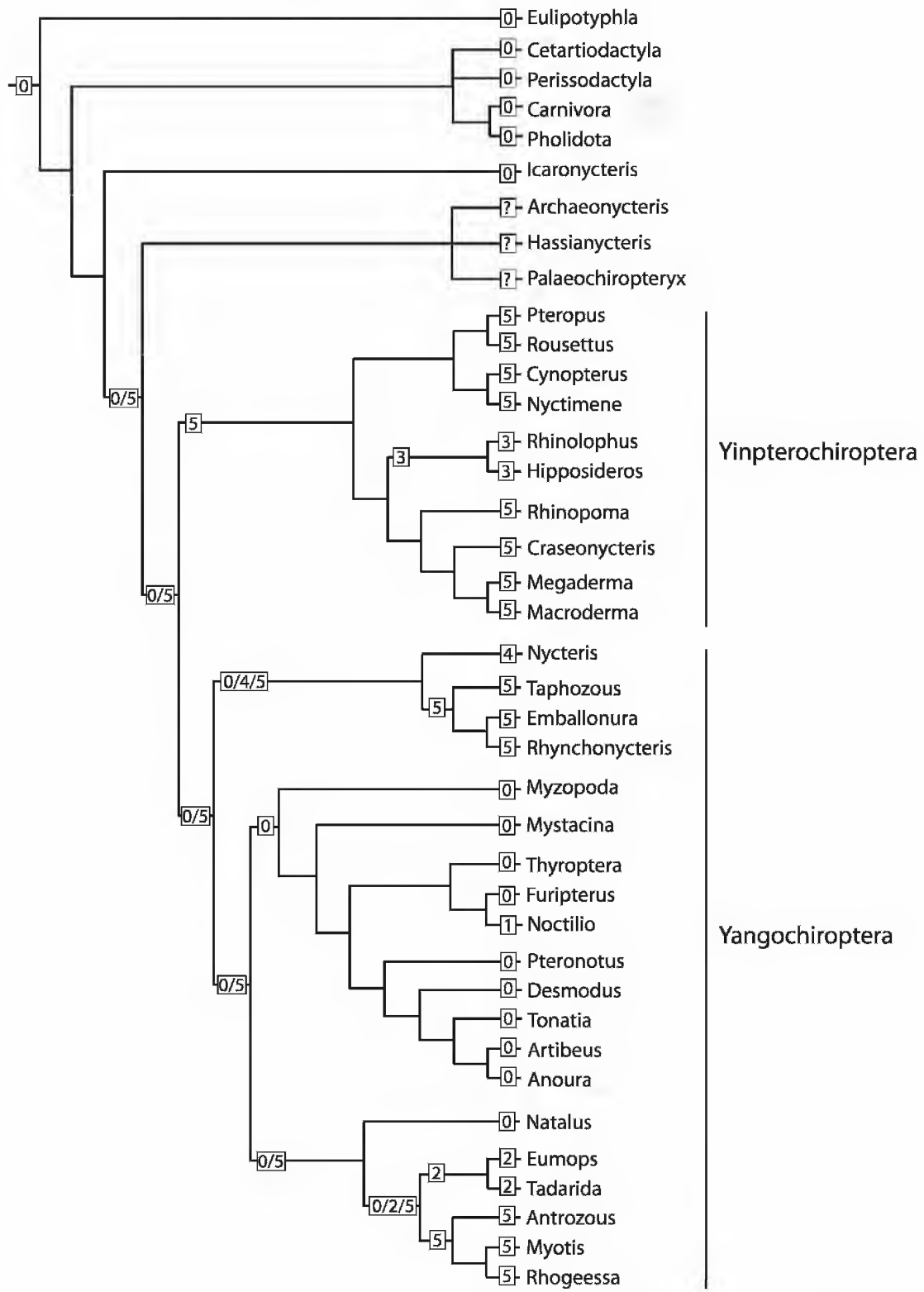


Fig. 33. Mapping of the third premaxillary character, palatine process of the premaxilla, onto the DNA tree of Teeling et al. (2005). See the text for definition of character states.

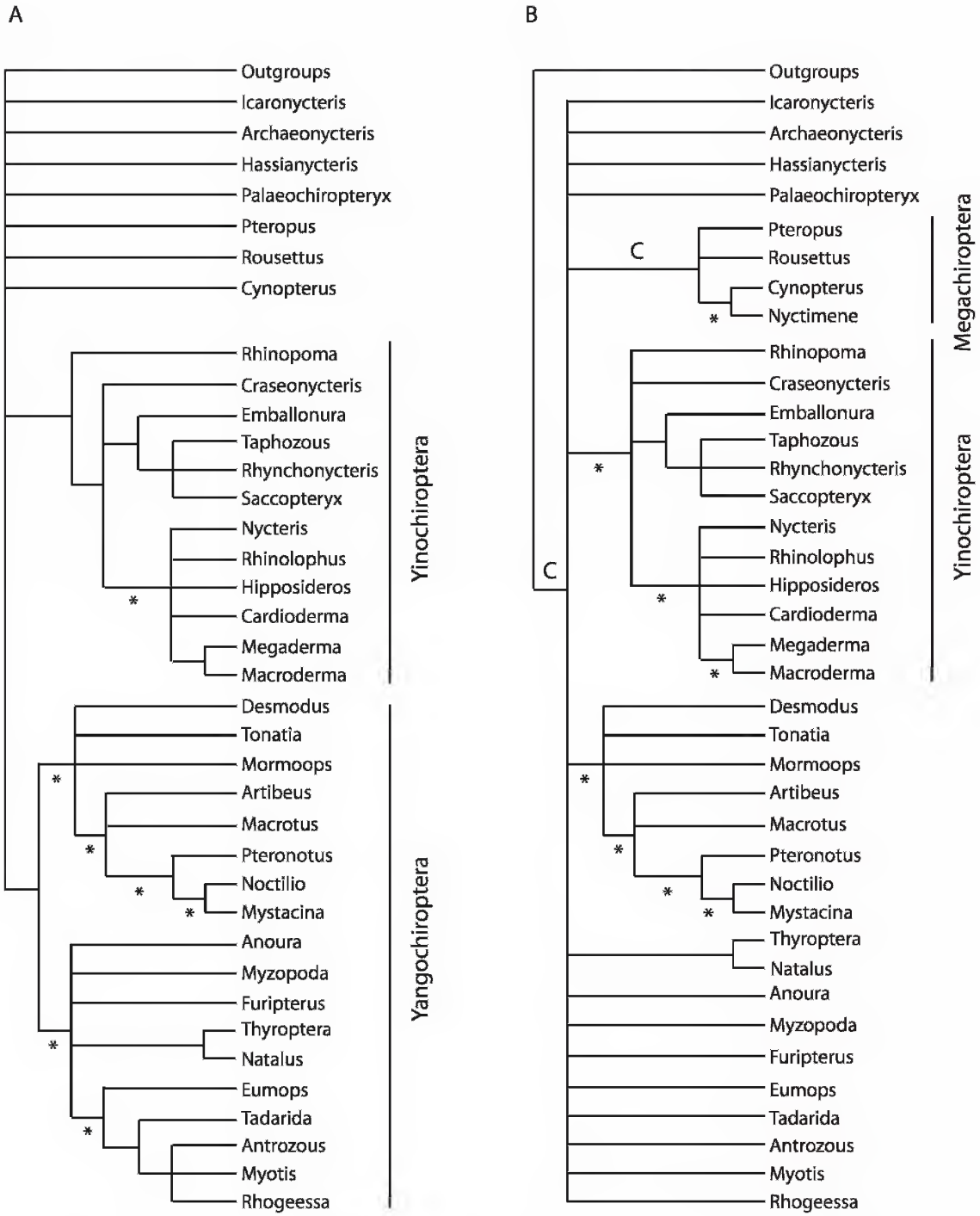


Fig. 34. Strict consensus of 810 optimal trees under implied weights based on premaxillary characters of this study (**A**), unconstrained search excluding *Nyctimene*; and strict consensus of 440 optimal trees, constrained search (constrained groups marked "C") under implied weights (**B**). Indicated with (*) are additional nodes recovered with respect to a corresponding analsysis of equal weights of the same data matrix.

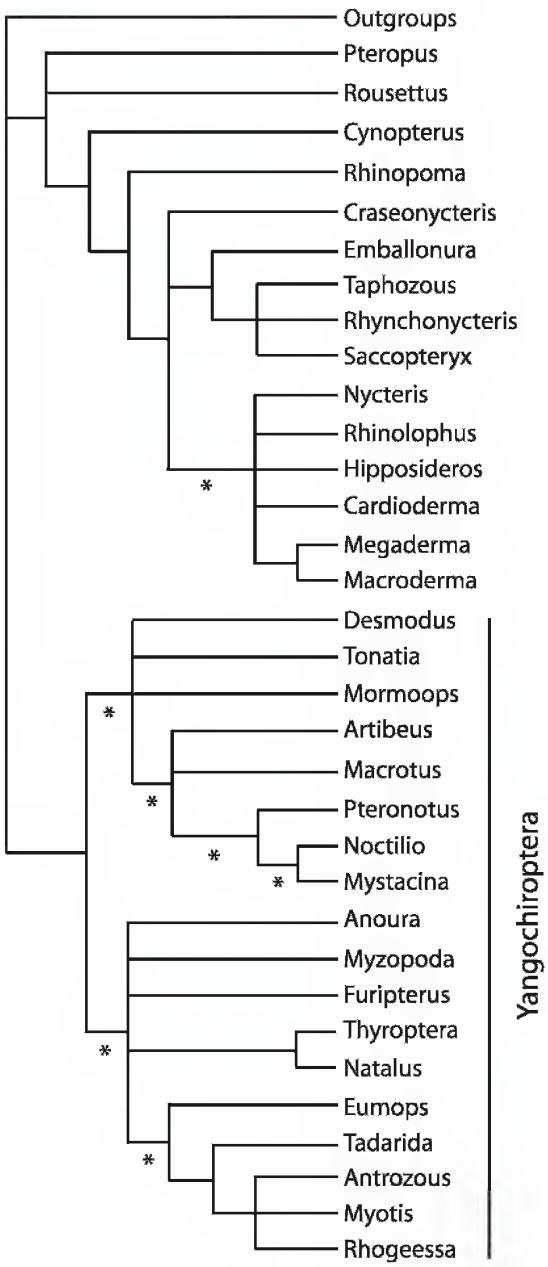


Fig. 35. Strict consensus of 36 trees under implied weights based on premaxillary characters of this study, unconstrained search excluding *Nyctimene* and the Eocene fossils *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, and *Hassianycteris*. Indicated with (*) are additional nodes recovered with respect to a corresponding analysis of equal weights of the same data matrix.

apparently occurred differently in the three parts of this bone in different bat lineages. This combination of features makes the premaxilla an important source of phylogenetic information (cf. Hutcheon and Kirsch, 2006), and at least 12 characters may be recognized that apply across all bats (plus at least three characters of more restricted application to particular bat groups). Our reexamination of the anatomy of the premaxilla requires a reassessment of its role in bat systematics, as previous assessments have overlooked key morphological differences among taxa, in some cases lumping together conditions that do not appear homologous on closer inspection.

Following Miller (1907), Koopman (1985) divided Microchiroptera into two infraorders that emphasized the apparent existence of two microbat morphotypes. These two groups appeared so distinct to Koopman that he named them after the Chinese concept of yin and yang, a metaphor encapsulating the extent of the perceived differences between the groups. The key anatomical feature supporting the microbat dichotomy is a premaxillary character that we call into question on the basis of our revision. Members of Yinochiroptera, as postulated by Miller (1907) and Koopman (1985), possess a "movable" premaxilla (i.e., the bone attaches to the maxilla via ligaments) and are grouped into seven families: nycterids, rhinolophids, hipposiderids, emballonurids, rhinopomatids, craseonycterids, and megadermatids. However, although in all of these families the maxilloincisive suture as a whole is a syndesmosis, the joint involves anatomically distinct parts of the premaxilla in different yinochiropterans. In the first three families listed earlier, the joint is formed between the *palatine* process and the maxilla, whereas in the last four families, the joint is formed between the *nasal* process and the maxilla. Actually, the premaxilla is "movable" only in hipposiderids and rhinolophids, in which a special type of joint is present (see the corresponding family accounts). In principle (but see later), these observations invalidate the diagnosis of Yinochiroptera sensu Koopman (1985), given that the grouping is based on a feature that is not homologous across all members of the

group. Obviously, this depends on our choice of treating anatomically distinct parts of the premaxilla in separate characters; however, those parts are so clearly distinguishable when examined in detail (compare, for instance, *Taphozous* and *Rhinolophus* in figs. 6 and 13) that the alternative treatment (the premaxilla as a whole) seems hardly defensible. Actually, both Koopman (1985, 1994) and Miller (1907) did distinguish a "palatal branch" from a "nasal branch" and used them individually as characters to diagnose or describe various bat taxa including families.

The case of the other infraorder, Yangochiroptera, is different. All members of this group share a complete premaxilla that is fused to maxilla in both parts of the maxilloincisive joint (nasal and palatine). Therefore, the anatomical basis of Yangochiroptera is correct from the perspective of homology. It is interesting to note that, whereas Yinochiroptera has been contradicted in all recent molecular studies (e.g., Eick et al., 2005; Teeling et al., 2000, 2005) and in one morphological study (in which Emballonuridae was found to lie outside this group; Simmons and Geisler, 1998), Yangochiroptera sensu Koopman (1985) has been consistently recovered in all recent phylogenies (e.g., Simmons, 1998; Simmons and Geisler, 1998; Teeling et al., 2000; Eick et al., 2005; Gunnell and Simmons, 2005; Teeling et al., 2005).

We redefined the basic premaxillary structure and coded it in new characters whose states represent the main structural variation seen in the chiropteran premaxilla (the body, nasal process, and palatine process; characters 1–3). We mapped each character onto the trees derived from the two latest iterations of current phylogenetic hypotheses of bat relationships: the morphology-based tree of Gunnell and Simmons (2005) and the DNA-based tree of Teeling et al. (2005). In the morphology tree, variation in our three premaxillary characters unambiguously supports many groupings, most notably Microchiroptera (character 1, state 3, if ordered, in spite of missing values in Eocene bats), Yinochiroptera (character 2, state 2), and Yangochiroptera sensu Koopman (1985; character 2, state 0). In the DNA tree, support exists only for extended Yangochiroptera (i.e., including Nycteridae and Emballonuridae; character 1, state 3) and Yangochiroptera sensu Koopman (1985; character 2, state 0).

In the light of the newly defined characters, the evolution of the nasal process in particular can be interpreted as an evolutionary process of either the weakening or the strengthening of the bone and the maxilloincisive joint. The nasal process is reconstructed as present with a foliate maxilloincisive suture in the ancestral bat (state 1; erroneously considered "cartilaginous" by Hutcheon and Kirsch, 2006). In the crown microbat clade, a dichotomy reminiscent of Koopman's premaxillary character is reconstructed. The $1 \rightarrow 2$ change in the yinochiropteran clade indicates a weakening of the nasal process, which is first attached to the maxilla via a syndesmosis and is later lost ($2 \rightarrow 4$) two nodes up in the tree at the base of the clade joining nycterids, megadermatids, rhinolophids, and hipposiderids. The opposite trend is seen in yangochiropterans, in which the $1 \rightarrow 0$ change can be interpreted as a strengthening of the joint via fusion with the maxilla. The DNA-based tree requires two independent events of premaxillary weakening, followed by three losses of the nasal process. From a functional perspective, it is interesting to note that mapping on either tree strongly suggests that loss of the nasal process was preceded by reduction, and that the latter is associated at least partially with the simplification of the maxilloincisive joint (from the complicated foliate suture, formed by interlocking laminae and deep recesses, to a joint in which the articulating surfaces are smooth and united only by ligaments).

The DNA-based tree requires ca. 45–300% more extra steps in the premaxillary characters mapped than does the morphological tree. To Hutcheon and Kirsch (2006), the higher number of extra steps in the molecular tree could be interpreted as proof of a high homoplasy level in morphology—so high as to make premaxillary characters phylogenetically unreliable and as to take this variation as positive evidence of adaptation in the premaxillary system (following Smith, 1993). They reached this conclusion despite the fact

that premaxillary variation does support important clades such as Yangochiroptera and many other groupings, regardless of what character definition or tree was used.

Beyond the major differences in structure discussed earlier, abundant additional variation in premaxillary structures among bats has been noted by previous authors and by ourselves. Part of that variation has been used phylogenetically in different case studies (e.g., Bogdanowicz and Owen, 1998; Dunlop, 1998; Hand and Kirsch, 1998; Wetterer et al. 2000; Carstens et al., 2002; Lim et al., 2004), and a wealth of new premaxillary characters is now available to help resolve the phylogenetic relationships of many bat groups. As a way to explore the relationships implied by these 16 new characters (12 informative at the level of Chiroptera with the current taxonomic sample), we performed parsimony analyses under equal and implied weights. Of course, with premaxillary characters alone, one can hardly expect a reasonable level of supported resolution and a high degree of congruence with analyses based on comprehensive data sets. In fact, only a few taxa (most notably *Nyctimene*, but also *Anoura*, *Mormoops*, and other bats) were recovered within extraneous clades. When analyzed in the absence of other data, if fossils are excluded, premaxillary characters group Pteropodidae with Yinochiroptera sensu Koopman (1985) on the basis of the lack of ossification of the palatine process (see fig. 35), which Simmons and Geisler (1998) listed as a synapomorphy of Chiroptera (see also fig. 32, cf. fig. 33). So despite the very low character-to-taxon ratio, several important groupings were recovered, depending on the analysis, including versions of the main microchiropteran clades (Yinochiroptera, Yangochiroptera, Rhinolophoidea, Noctilionoidea), some of the polytypic families (Emballonuridae and Vespertilionidae), and a version of Yinpterochiroptera that includes all traditional yinochiropteran taxa.

In view of these results, we disagree with Hutcheon and Kirsch (2006: 6) in their statement that the premaxilla as a character source "is not a particularly useful one for phylogeneticists". The fact that premaxillary characters, in isolation from other evidence, do not by themselves recover the expected molecular topology, or do not map that topology exactly, in no way invalidates their importance as a character source. Rather, the relevance of a character or character complex with respect to a phylogenetic hypothesis in particular ultimately can be assessed only in the presence of other characters—that is, by character congruence in a simultaneous analysis (Nixon and Carpenter, 1996). This is because inclusion of a character can lead to modification of the current phylogenetic hypothesis (i.e., a different tree may become optimal when the character is added). Thus, while character mapping is a useful exploratory tool, dismissal of morphological (or other) evidence solely on that basis is a misguided approach, as is the dismissal of a character system under the failed expectation of perfect performance. Homoplasy exists in all character systems, so a single character system cannot be decisive about the phylogenetic relationships of an entire group, especially one as complex as Chiroptera.

In conclusion, based on a character redefinition that is in closer accordance with anatomical premaxillary structures than previously used characters, we have shown that part of the variation seen in this bone across bat taxa is congruent with phylogenetic patterns discovered analyzing comprehensive data sets, and more so when morphology-based topologies are considered. Part of the variation conflicts with groupings derived from molecular analyses, though. Still, some suprafamilial and suprageneric clades present in all major phylogenetic analyses are indeed supported by premaxillary character states—most notably, Yangochiroptera. Mapping of the main structural characters on current phylogenetic hypotheses has shown that the evolution of the premaxilla can be interpreted as a process toward strengthening via fusion to the maxilla in some clades or toward the opposite—weakening via reduction of structures and simplification of joints—in other clades. The chiropteran premaxilla is a richer character source than previously thought, and we suggest that variation in this bone be explored further and used in bat phylogenetics and systematics.

ACKNOWLEDGMENTS

We thank Larry Heaney (Field Museum of Natural History, Chicago), Rubén Barquez (Colección Mamíferos Lillo, Tucumán, Argentina), John R. Wible (Carnegie Museum of Natural History, Pittsburgh), Mark Engstrom and Burton Lim (Royal Ontario Museum, Toronto), Mark Hafner (Louisiana State University Museum of Natural Science, Baton Rouge), and Linda Gordon (U.S. National Museum of Natural History, Washington, D.C.) for access to specimens used in this study. Thanks also to Tim Rowe and the staff of the University of Texas CT Lab for help with scanning and image processing. Special thanks to John R. Wible and Jonathan H. Geisler, whose thorough reviews greatly improved the manuscript. Funding for this report was provided by the National Science Foundation (Research Grants DEB-9873663 and EF-0629811 to N.B.S.) and AMNH Coleman and Vernay Postdoctoral fellowships to Norberto P. Giannini.

REFERENCES

Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. Volume I: Megachiroptera. London: Trustees British Museum (Natural History).

Bergmans, W. 1997. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899, and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. Beaufortia 47: 11–90.

Bogdanowicz, W., and R. Owen. 1998. In the Minotaur's labyrinth. Phylogeny of the bat family Hipposideridae. *In*: T.H. Kunz and P.A. Racey (editors), Bat biology and conservation: 27–42. Washington, DC: Smithsonian Institution Press.

Bouchard, S. 1998. Chaerephon pumilus. Mammalian Species 574: 1–6.

Bouchard, S. 2001. Chaerephon ansorgei. Mammalian Species 660: 1–3.

Carstens, B.C., B.L. Lundrigan, and P. Myers. 2002. A phylogeny of the Neotropical nectar-feeding bats (Chiroptera: Phyllostomidae) based on morphological and molecular data. Journal of Mammalian Evolution 9(1/2): 23–53.

Dunlop, J.M. 1998. The evolution of behaviour and ecology in Emballonuridae (Chiroptera). Ph.D. dissertation, York University: North York, Ontario.

Eick, G.N., D.S. Jacobs, and C.A. Mathee. 2005. A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). Molecular Biology and Evolution 22: 1869–1886.

Evans, H.E. 1993. Miller's anatomy of the dog, 3rd ed. Philadelphia: W.B. Saunders.

Fenton, M.B., and J.L. Eger. 2002. Chaerephon chapini. Mammalian Species 692: 1–2.

Giannini, N.P., and N.B. Simmons. 2005. Conflict and congruence in a combined DNA-morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). Cladistics 21: 411–437.

Giannini, N.P., and N.B. Simmons. 2007. Element homology and the evolution of dental formulae in megachiropteran bats (Mammalia: Chiroptera: Pteropodidae). American Museum Novitates 3559: 1–27.

Giannini, N.P., J.R. Wible, and N.B. Simmons. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bulletin of the American Museum of Natural History 295: 1–134.

Goloboff, P.A. 1993. Estimating character weights during tree search. Cladistics 9: 83–91.

Goloboff, P.A., J.M. Carpeneter, J.S. Arias, and D.R. Miranda Esquivel. In press. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics

Goloboff, P.A., J.S. Farris, and K. Nixon. 2004. T. N. T.: tree analysis using new technologies. Program and documentation. Available at www.cladistics.org.

Gregorin, R., and A.D. Ditchfield. 2005. New genus and species of nectar-feeding bat in the tribe Lonchophyllini (Phyllostomidae: Glossophagine) from northeastern Brazil. Journal of Mammalogy 86: 403–414.

Gunnell, G.F., and N.B. Simmons. 2005. Fossil evidence and the origin of bats. Journal of Mammalian Evolution 11: 257–277.

Hand, S.J., and J.A.W. Kirsch. 1998. A southern origin for the Hipposideridae (Microchiroptera)? Evidence from the Australian fossil record. *In*: T.H. Kunze and P.A. Racey (editors), Bat biology and conservation: 72–90. Washington, DC: Smithsonian Institution Press.

Hill, J.E. 1963. A revision of the genus *Hipposideros*. Bulletin of the British Museum (Natural History) 2(1): 1–129.

Hill, J.E. 1974. A new family, genus, and species of bat (Mammalia: Chiroptera) from Thailand. Bulletin of the British Museum of Natural History Zoology 27: 301–336.

Hill, J.E. 1982. A review of the leaf-nosed bats *Rhinonycteris*, *Cloeotis* and *Triaenops* (Chiroptera: Hipposideridae). Bonner Zoologische Beitrage 33: 165–186.

Hill, J.E., and S.E. Smith. 1981. Craseonycteris thonglongyai. Mammalian Species 160: 1–4.

Hutcheon, J.M., and J.A.W. Kirsch. 2006. A movable face: deconstructing the Microchiroptera and a new classification of extant bats. Acta Chiropterologica 8(1): 1–10.

Jepsen, G.L. 1966. Early Eocene bat from Wyoming. Science 154: 1333–1339.

Koopman, K.F. 1985. A synopsis of the families of bats, part VII. Bat Research News 25: 25–29. [dated 1984 but issued 1985]

Koopman, K.F. 1994. Chiroptera systematics. Handbook of Zoology [vol. 8, part 60]: Mammalia. New York: Walter de Gruyter.

Lim, B.K., M.D. Engstrom, N.B. Simmons, and J.M. Dunlop. 2004. Phylogenetics and biogeography of least sac-winged bats (*Balantioteryx*) based on morphological and molecular data. Zeitschrift für Säugetierkunde 69: 225–237.

Macrini, T.E., T. Rowe, and M. Archer. 2006. Description of a cranial endocast from a fossil platypus, *Obdurodon dicksoni* (Monotremata, Ornithorhynchidae), and the relevance of endocranial characters to monotreme monophyly. Journal of Morphology 267: 1000–1015.

Miller, G.S., Jr. 1907. The families and genera of bats. Bulletin of the United States National Museum 57: 1–282.

Nixon, K.C., and J.M. Carpenter. 1996. On simultaneous analysis. Cladistics 12: 221–241.

Romagnoli, M.L., and M.S. Springer. 2000. Evolutionary relationships among Old World fruitbats (Megachiroptera: Pteropodidae) based on 12S rRNA, tRNA valine and 16S rRNA gene sequences. Journal of Mammalian Evolution 7: 259–284.

Rowe, T.B., T.P. Eiting, T.E. Macrini, and R.A. Ketcham. 2005. Organization of the olfactory and respiratory skeleton in the nose of the Gray Short-tailed Opossum *Monodelphis domestica*. Journal of Mammalian Evolution 12(3/4): 303–335.

Simmons, N.B. 1994. The case for chiropteran monophyly. American Museum Novitates 3130: 1–54.

Simmons, N.B. 1998. A reappraisal of interfamilial relationships of bats. *In*: T.H. Kunz and P.A. Racey (editors), Bats: phylogeny, morphology, echolocation, and conservation biology: Washington: Smithsonian Institution Press.

Simmons, N.B. 2005. Order Chiroptera. *In*: D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 3rd ed.: 312–529. Washington DC: Smithsonian Institution Press.

Simmons, N.B., and T.M. Conway. 2001. Phylogenetic relationships of mormoopid bats (Chiroptera: Mormoopidae) based on morphological data. Bulletin of the American Museum of Natural History 258: 1–97.

Simmons, N.B., and J.H. Geisler. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bulletin of the American Museum of Natural History 235: 1–182.

Smith, J.D., and G. Storch. 1981. New Middle Eocene bats from the "Grube Messel" near Darmstadt, W-Germany (Mammalia: Chiroptera). Senckenbergiana Biologica 61: 153–168.

Smith, K.K. 1993. The form of the feeding apparatus in terrestrial vertebrates: studies of adaptation and constraint. *In*: J. Hanken and B.K. Hall (editors), The skull: functional and evolutionary mechanisms. Volume 3: 150–196. Chicago: University of Chicago Press.

Springer, M.S., L.J. Hollar, and J.A.W. Kirsch. 1995. Phylogeny, molecules versus morphology, and rates of character evolution among Fruit bats (Chiroptera: Megachiroptera). Australian Journal of Zoology 43: 557–582.

Storch, G., B. Sigé, and J. Habersetzer. 2002. *Tachypteron frenzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). Paläontologische Zeitschrift 76(2): 189–199.

Sudman, P.D., L.J. Barkley, and M.S. Hafner. 1994. Familial affinity of *Tomopeas ravus* (Chiroptera) based on protein electrophoretic and cytochrome B sequence data. Journal of Mammalogy 42: 152–159.

Teeling, E.C., M. Scally, D. Kao, M. Romagnoli, M.S. Springer, and M.J. Stanhope. 2000. Molecular evidence regarding the origin of echolocation and flight in bats. Nature 403: 188–192.

Teeling, E.C., M.S. Springer, O. Madsen, P. Bates, S.J. O'Brien, and W.J. Murphy. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307: 580–584.

Wetterer, A.L., M.V. Rockman, and N.B. Simmons. 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. Bulletin of the American Museum of Natural History 248: 1–200.

Wible, J.R., and M.J. Novacek. 1988. Cranial evidence for the monophyletic origin of bats. American Museum Novitates 2911: 1–19.

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site http://library.amnh.org/pubs. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).